THE MATERNAL BEHAVIOUR OF THE PIG IN THE FARROWING CRATE

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I hereby declare that this thesis is of my own composition, and that all assistance has been duly acknowledged. The results presented herein have not previously been submitted for any other degree or qualification.

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LITERATURE REVIEW:

THE MATERNAL BEHAVIOUR OF THE PIG IN THE FARROWING CRATE

Introduction

Reducing piglet pre-weaning mortality, in commercial pig production systems, has remained a consistent problem for those in the pig industry for many years (Braude *et al.*, 1954; Gracey, 1955; Sadana and Singh, 1972; Nielsen *et al.*, 1974; English and Edwards, 1996). Many studies have looked at how changes in the way the sow and her litter are managed can reduce piglet mortality (Asdell and Willman, 1941; Lee, 1977; Edwards and Furniss, 1988; English and Edwards, 1996; Straw *et al.*, 1998). However, even within studies with similar management strategies, the distribution of piglet mortality between litters is not random (Bel Isle and England, 1978; Maddock, 1980; Dyck and Swierstra, 1987; Fraser *et al.*, 1988; de Passille and Rushen, 1989). Thus, some litters are more prone to mortality than others (de Passille and Rushen, 1989; Fraser, 1990). It has been recognised that current knowledge on the litter risk factors for piglet mortality is extremely limited (Fraser, 1990). One of the more important litter risk factors influencing piglet mortality is likely to be the maternal behaviour of the sow. However, it is not known to what extent differences in the behaviour of the sow towards her piglets can influence piglet mortality in the farrowing crate.

The Farrowing Crate and its Influence on Piglet Mortality

The farrowing crate is designed to reduce crushing mortalities by minimising the uncontrolled descent of the sow's hind quarters when the sow lies down from a standing position (Green, 1981; English *et al.*, 1982: p. 135; Baxter, 1984: p. 455). The farrowing crate system also allows more human intervention during parturition than what is possible in the farrowing pen system. Human intervention during parturition, such as assisted birthing and drying the newly born piglet, is often quoted as a strategy that helps to reduce piglet mortality (English and Morrison, 1984; English and Edwards, 1996; Nickerson, 1996; Hacker, 2000). However, for some sows human intervention may actually increase the risk of piglet crushing if the disturbance results in an increase in sow posture changing. This may explain why a large scale survey of farrowing systems (Gustaffsson, 1983) found no difference in piglet mortality between pen and the crate systems, whilst controlled experiments have found lower mortality in the crate (Devilat *et al.*, 1971; Aherne, 1982; Collins *et al.*, 1987).

Crushing is the most common cause of piglet mortality in commercial pig production, and remains so even when crates are used (Baxter, 1971; Glastonbury, 1977; Bolet, 1982; Friendship *et al.*, 1986; Spicer *et al.*, 1986; Svendsen *et al.*, 1986; Weary *et al.*, 1998). The incidence of crushing amongst numbers born alive in farrowing crates varies widely between different studies (9.2%, Blackshaw *et al.*, 1994; 4.6%, Lou and Hurnik, 1994; 25%, Arey and Sancha, 1996). Farrowing crates limit the number of crushing mortalities by reducing the speed and frequency with which posture changes, such as lying down from a standing position (Baxter, 1984: p. 455) and rolling into a side lying posture (Weary *et al.*, 1996a), take place.

The savaging of piglets by the sow is another type of piglet mortality seen in commercial pig production, which tends to occur during the sows first parturition (van der Steen *et al.*, 1988). Savaging occurs in both the farrowing crate and the farrowing pen but there is some data published that suggests that the incidence of savaging may be more common in crated sows (Cronin *et al.*, 1996). The killing of offspring in the captive environment has often been viewed as a pathological behaviour brought on by various aspects of the artificial environment (Eisenberg,

1981: p. 398; Fraser and Broom, 1990: p. 223). The incidence of piglet-directed aggression from sows housed in farrowing crates varies greatly between studies, probably due to different definitions of aggression (8%, Knap and Merks, 1987; 50%, Cronin *et al.*, 1994; 21%, Alhstrom, 1997; 29%, Calvert, 1997).

The Maternal Behaviour of the Sow

In open farrowing systems the sow can perform her full compliment of maternal behaviours. As gestation nears the end, the behaviour of the free-ranging sow changes and she starts to spend increasing amounts of time away from other pigs as the process of selecting a nest site begins. Grundlach (1968) reports that this process begins one week before parturition, whilst Jensen (1988) has suggested that isolation and nest site seeking occurs one to two days prior to parturition. Having selected a nest site, that offers some shelter but with an open view to aid vigilance (Grundlach, 1968; Signoret *et al.*, 1975; Stolba and Wood-Gush, 1989), nest-building starts. Jensen (1993) identified two distinct types of nest-building behaviour using factor analysis. These were preparatory behaviour such as standing, nosing and rooting the floor, thought to be influenced by internal cues (Jensen, 1993), and nest material manipulation, which, based on the absence of vacuum carrying and arranging in barren environments, is thought to require external cues (Jensen, 1993). The preparatory part of nest-building behaviour can be induced artificially by administering prostaglandin-$F_{2\alpha}$ to pseudopregnant gilts (Boulton *et al.*, 1997), demonstrating that this behaviour is internally driven. The thwarting of nest-building motivation is thought to be responsible for the higher cortisol concentrations found in crated compared to penned sows during the nest-building phase (Lawrence *et al.*, 1994). This result suggests that sows in crates attempting to nest-build suffer an aversive psychological state (Lawrence *et al.*, 1997), which compromises the sow's welfare.

Following the onset of parturition, sows tend to be very passive and spend a lot of time lying on their sides (Signoret *et al.*, 1975; Bøe, 1994). This is an essential part

of sow maternal behaviour since piglets are born with very limited energy reserves (English and Morrison, 1983) and so must seek out their mothers milk soon after birth. Unlike many other farm animals, sows do not tend to help their piglets free themselves from placental membranes, umbilical cord or clean off any birth fluids (Signoret *et al.*, 1975; Graves, 1984; Fraser and Broom, 1990: p. 218). Given the chance, sows will usually ingest the placenta after expulsion (Signoret *et al.*, 1975; Graves, 1984; Fraser and Broom, 1990: p. 218) but in the farrowing crate this is rarely possible. In rats, the attractiveness of the placenta for ingestion depends on the proximity to parturition, and so probably the hormonal state of the animal (Kristall, 1991). Placentophagia may also help to hasten the onset of maternal behaviour in rats (Kristall, 1981), however, this effect may be mediated through increased contact with the pups as the birth membranes are licked off. Sow-piglet nose to nose contacts are a characteristic of sow maternal behaviour and are thought to be essential for the development of mother-offspring bonds (Whatson and Bertram, 1983; Jensen and Redbo, 1987). The sow may also kick out with her hind legs during parturition, an action that some have attributed the function of helping the piglets find the udder (Herskin *et al.*, 1998).

The first meal of milk and colostrum the piglet receives is obtained freely, without the need for teat massage (Castren *et al.*, 1992), so initially piglets will suckle from many teats in turn (de Passille and Rushen, 1989). A regular pattern to suckling soon develops, whereby milk is only available during short time periods and then at all teats at the same time (Fraser, 1980; Ellendorff *et al.*, 1982; Castren *et al.*, 1992). Piglets also develop teat fidelity (Fraser, 1975) and the behaviour of the litter as a whole becomes more synchronised over time (de Passille *et al.*, 1988; de Passille and Rushen, 1989). In fact, litters that show a low degree of synchronicity tend to be those with a high risk of mortality (de Passille and Rushen, 1989). The lack of synchronicity is due to uncompetitive piglets with poor initial weight gains remaining close to the sows udder between suckling bouts (de Passille and Rushen, 1989; Weary *et al.*, 1996b).

Weaning is a gradual process in free-ranging domestic pigs (Newberry and Wood-Gush, 1985; Jensen and Recen, 1989; Bøe, 1991), completed by seventeen weeks of age (Jensen, 1988) and occurring at a mean age of 82 days (Stolba, 1982). In loose-housed husbandry systems where the sow is allowed to leave her piglets in the nest, there is considerable variation in the age at which they wean their piglets (Bøe, 1994). This may be due to a problem inherent with the husbandry system, for instance, the sow might expect her piglets to follow her after nine to ten days (Jensen and Redbo, 1987) but a gate prevents this from happening, leading to the sow becoming disinterested in her piglets (Bøe, 1994). Alternatively, the variation in chosen weaning age may reflect differences between sows in their maternal quality. In husbandry systems where the sow is not free to leave her piglets, weaning usually takes place between 19 and 32 days (English and Edwards, 1996). Over the last 20 years there has been a trend towards earlier weaning (English and Edwards, 1996) but current welfare guidelines recommend weaning at no earlier than three weeks of age (Ministry of Agriculture, Fisheries and Food, 1983).

Sow Maternal Behaviour as a Piglet Mortality Risk Factor

Many studies that have explored the effect of sow behaviour on piglet crushing have focussed on the types of posture change that result in piglet crushing. In farrowing crates, lying down from a standing or sitting posture results in the most crushings (Edwards *et al.*, 1986), whilst stepping on piglets (Olsson and Svendsen, 1989) and moving from a lie to a sit posture (Weary *et al.*, 1996a) can also cause piglet crushings. In open farrowing systems, lying down from standing also causes a lot of crushings but especially lying down to a lateral (side) lying posture (Marchant *et al.*, 1996; Wechsler and Hegglin, 1997). In addition rolling onto the side from an upright (ventral) lying posture or switching sides can also result in piglet crushings in farrowing pens (Marchant *et al.*, 1997; Wechsler and Hegglin, 1997). Other studies have studied the sows behaviour in relation to crushing in more detail. Marchant *et al.* (1996) found that, for sows in farrowing pens, the strategy of lying down quickly and being attentive to where piglets are prior to lying results in the fewest crushings

and near-crush events. Subsequently, Wechsler and Hegglin (1997) found that a behavioural score based on the frequency with which sows made dangerous posture changes could predict risk of crushing from current and earlier lactations. This suggests that sows are consistent over parities in their risk of crushing and that this might be due to a consistent maternal style.

If a piglet is laid upon by a sow, it stands a good chance of surviving if the piglet frees itself or if the sow moves off the piglet within one minute (Weary *et al.*, 1996a). Therefore, one way a sow might reduce the risk of her crushing a piglet to death is to be alert to piglet alarm calls. The playback of a piglet scream causes sows to respond by changing posture, looking at the speaker or increasing the time taken to lie, whilst visual and tactile piglet cues have no such effect (Hutson *et al.*, 1991; Hutson *et al.*, 1993). The higher the volume of the piglet call, the more responsive the sow is (Hutson *et al.*, 1993), suggesting that this is an honest signal of piglet need. Individual variation in the response of sows to a piglet alarm call is large, with only approximately 60% of sows responding to calls (Hutson *et al.*, 1991; Cronin and Cropley, 1991). This has led to speculation that there might be genetic variation in this trait that could be utilised in selection programmes (Hutson *et al.*, 1991). Wechsler and Hegglin (1997) later found that the individual variation in the responsiveness of sows of a piglet squeal was correlated to the percentage of crushing deaths during the current and previous lactations. However, despite attempts to use the squeal test to predict a sow's risk of crushing for selection experiments (e.g. Rhydmer *et al.*, 1998; Thodberg *et al.*, 1998; Grandinson *et al.*, 2000), the correlation between responsiveness to the piglet squeal and the incidence of crushing has yet to be repeated. A sow's responsiveness to a piglet squeal has only a moderate repeatability (0.25) when measured over subsequent parities (Rhydmer *et al.*, 2000), which puts an upper limit on the heritability of responsiveness as a sow trait (Simm, 1998: p. 129).

The heritability of crushing, as a sow trait, is unknown. However, the heritability of savaging, a type of mortality that by definition is influenced by sow behaviour, has been estimated. Knap and Merks (1987) report a high heritability lying between 0.4

and 0.9, whilst van der Steen (1988) report a lower heritability lying between 0.12 and 0.25. These heritability values make artificial selection against piglet savaging possible.

There have been very few studies of the behaviour of savaging sows. Consequently, the causation of savaging remains a mystery (Fraser, 1990). Hansen and Curtis (1981) report that during 48 hours prior to parturition, savaging sows would stand or sit up (breaking a light beam) more frequently than non-savaging sows. First parity sows that savage are identified during the first few hours following the birth of the first piglet by lying ventrally more and standing more, and by being generally more restless, than non-savaging gilts (Ahlstrom, 1997). An increased likelihood of responding to piglets is also thought to be a characteristic of savaging gilts (Ahlstrom, 1997; Calvert, 1997). The provision of nesting substrates prior to parturition promotes sow-piglet interactions and responsiveness to piglet squeals (Cronin and van Amerongen, 1991; Cronin and Smith, 1992; Herskin *et al.*, 1998), whilst nesting substrates are claimed to reduce the incidence of savaging (Brummer, 1972; Sambraus, 1976). However, nesting substrates are unlikely to achieve this effect if savaging is associated with increased sow-piglet interactions.

In other species, whether females react aggressively towards young or attempt to care for young depends on the hormonal state of the female (rat: Pederson *et al.*, 1982; gerbil: Elwood and Ostermeyer, 1984; ewe: Poindron *et al.*, 1984). The appropriate experiments to find out whether this is also the case in pigs have yet to be run. However, it is likely that a sow's reaction towards piglets is also influenced by her hormonal state. It has been suggested that a hormonal miscue at parturition, possibly caused by a pre-parturient stressor, might be responsible for piglet savaging (Fraser, 1990).

The Biological Basis of Individual Variation in Behaviour

Most behaviours, within a population of the same species, sex and age, display considerable individual variation which is frequently viewed as just statistical noise. However, functional and evolutionary analysis would suggest that much of the variation has been maintained by Darwinian evolution (van Oortmerssen and Busser, 1989; Martin and Bateson, 1993: p. 43; Mendl and Deag, 1995). Targeted artificial selection can accentuate these differences. Thus, bi-directional selection for life-span in *Drosophila melanogaster* has resulted in highly fecund individuals that die young and less fecund individuals that live much longer (Rose and Charlesworth, 1981). Similarly, bi-directional selection for attack latency in mice has resulted in lines of mice with divergent ways of coping with different challenging situations (Benus *et al.*, 1991; Sluyter *et al.*, 1996).

In aversive situations individual differences in behaviour are linked to physiological measures and the differences seen are sometimes consistent over time (Lyons and Price, 1986; Bohus *et al.*, 1987; Lawrence *et al.*, 1991; Terlouw *et al.*, 1997). The behaviour of individual pigs in one situation can often be used to predict the behaviour of the pig in another situation (von Borell and Ladewig, 1992). The behavioural style observed being correlated to the cortisol response following adrenocorticotrophin hormone (ACTH) challenge, indicating differences in the sensitivity of the hypothalamic pituitary adrenal (HPA) axis (von Borell and Ladewig, 1992). The extent to which pigs drink excessively or perform stereotypic chain chewing in response to tethering, is related to the sensitivity of the central dopaminergic system (Terlouw *et al.*, 1992). Behavioural differences in mice have been also been correlated to central dopaminergic sensitivity (Bohus, 1988), as well as the abundance of arginine-vasopressin immunoreactive neurones in the suprachiasmatic nucleus (Sluyter *et al.*, 1995) and anatomical differences in the hippocampus (Hausheer-Zamakupi *et al.*, 1996). Therefore much of the behavioural and physiological variability seen has its basis in fundamental differences in the central nervous system (Terlouw *et al.*, 1997), which are candidates through which genetic selection may be mediated (Sluyter *et al.*, 1996).

Genetic Variation in Maternal Behaviour and Quality

Evidence for genetic variation in maternal behaviour and overall maternal quality come from experiments on mice with targeted gene deletions (e.g. see Keverne, 1997 for a review; Lefebvre *et al.*, 1998). Genetic variation in sow maternal behaviour and overall quality is suggested by pig breed studies.

The Chinese Meishan pig breed is renowned for the superior mothering qualities and docility of its sows compared with the European commercial breeds (Schouten and Meunier-Salaun, 1990). Cross-fostering experiments have shown that Meishan mothers have improved piglet survival and piglet growth rates compared to European commercial breeds (van der Steen and de Groot, 1992; Sinclair *et al.*, 1996, 1998). Furthermore, piglet growth rate in Meishan litters improves over the first few parities whereas in the Large White breed there is no such improvement (Sinclair *et al.*, 1996). The better mothering qualities of Meishan sows is partly due to a higher quality of milk (Zou *et al.*, 1992) and partly due to the sows spending more time nursing their piglets than Large White sows (Schouten and Meunier-Salaun, 1990; Sinclair *et al.*, 1998).

Behavioural ecology theories state that animals will trade-off current reproductive effort with future reproductive effort (Clutton-Brock, 1991: pp. 31-46). Breed differences may exist for the emphasis placed on current reproductive effort over future reproductive effort. Sinclair *et al.* (1996) demonstrated that Meishan sows catabolize their greater fat reserves to support milk output, and that this is facilitated by a high protein diet. The apparent cost of putting so much effort into the current lactation is to increase the next weaning to conception interval. Thus, Large White sows tend to use the higher protein diet to minimise their own weight loss, rather than improve milk production, thus reducing their next weaning to conception interval (Sinclair *et al.*, 1996). Thus it would appear that Meishan sows put relatively more emphasis on current reproductive effort, whilst the Large White breed puts relatively more emphasis on future reproductive potential. After about the fourth parity, Meishan sows appear to reduce their investment in lactation because the mean

weight gain of their litters, from birth to weaning, declines (Yen, 1999). Equivalent information is not readily available for Large White sows but Cozler *et al.* (1998) reported that after parity two, the survival rate of piglets from Large White-Landrace sows remained constant. This suggests that maternal investment from Large White-Landrace sows remains constant after parity two. Comparison of domestic sows with wild boar crosses has indicated that domestication has resulted in sows that invest more in the current litter (Gustafsson *et al.*, 1999). However, variation in a sow's lifetime reproductive strategy would appear to exist between highly domesticated breeds.

The Meishan sow is also known for its larger litter sizes (Bidanel *et al.,* 1989), between three and four more piglets weaned per litter than for Large White sows (Haley and Lee, 1993). The unborn Meishan foetuses tend to have improved pre-natal survival (Ashworth *et al.*, 1994; Youngs *et al.*, 1994) but are born small in comparison to European commercials (van der Steen and de Groot, 1992; Sinclair *et al.*, 1996). Despite being smaller than European commercial newly born piglets, Meishan piglets tend to have better developed adipose cells which may improve their chances of survival by assisting with thermoregulation (Herpin *et al.*, 1993). However, recent research has shown that the higher litter weights produced by Meishan synthetics (50% Meishan genes) are due solely to maternal effects rather than litter size or piglet genotype (Haley and Lee, 1993; Sinclair *et al.*, 1998).

Nest building is another aspect of maternal behaviour but the evidence for breed differences here is less conclusive. Meunier-Salaun *et al.* (1991) reported that Meishan sows would spend more time in floor-directed exploratory behaviour 24 hours pre-farrowing than Large White sows. However, this behavioural difference was only found in farrowing crates, whilst in straw pens there were no breed differences in pre-farrowing substrate-directed (straw, floor or fixtures) behaviour (Schouten and Meunier-Salaun, 1990). These findings suggest that the expression of nest-building behaviour is influenced by the environment in different ways for the two different breeds. This may be due to differences in between the two breeds in how they adapt nest-building behaviour to the farrowing crate environment.

Alternatively, the difference between the two breeds in the first study may be simply due to the Meishan sow having relatively more space in a standard farrowing crate on account of the Meishan sow being smaller than the Large White.

The Adaptive Abilities of Different Breeds

When introduced to a novel environment, Meishan grower pigs have much lower levels of locomotion than the Large White breed which display more active exploratory behaviour (Mormede *et al.*, 1984). Meishan pigs are also slower to feed in a neophobia test after 24 hours food deprivation (Mormede *et al.*, 1984). More recently, Desautes *et al.* (1997) compared the behavioural and physiological responses to environmental challenge of Meishan and Large White pigs and their F1 and F2 crosses. They found that low defecation, vocalisation and locomotion scores in Meishan pigs compared to Large White pigs, with the F1 crosses having intermediate scores. These results suggest that Meishan pigs were relatively indifferent to the novel environment (Desautes *et al.*, 1997). Furthermore, the F1 crosses had intermediate scores for these behavioural measures indicating autosomal inheritance (Desautes *et al.*, 1997). In contrast with the behaviour of Meishan pigs, the physiology of Meishan pigs in response to environmental challenge tells a different story. The hypothalamic-pituitary-adrenal (HPA) axis is hypersensitive to environmental challenge in Meishan compared to Large White (Bergeron *et al.*, 1996, Desautes *et al.*, 1997). Hypersensitivity of the HPA axis is also found in F1 and F2 Meishan-Large White crosses, suggesting that this is a dominant trait associated with Meishan genes (Bergeron *et al.*, 1996, Desautes *et al.*, 1997). These breed differences when faced with an environmental challenge may reflect differential adaptive abilities (Mormede *et al.*, 1984; Meunier-Salaun *et al.*, 1991; Bergeron *et al.*, 1996). With the higher HPA activity in Meishan pigs indicating possible problems in coping with certain aspects of the environment.

Both locomotory activity and HPA activity in a novel environment, displayed a continuous distribution in the F_2 generation indicating the involvement of multiple

genes with additive effects (Plomin *et al.*, 1990; Mormede *et al.*, 1994). However, low locomotor activity and high HPA activity appear to be only fortuitously associated in Meishan pigs since only weak correlations are found in the F2 segregating crosses of Meishan and Large White (Mormede *et al.*, 1994; Desautes *et al.*, 1997). This points to the possibility of selecting for one of these traits without automatically selecting the other.

Adaptation to the Farrowing Crate

Genes can be seen to set up behavioural predisposition's to act in certain ways. In terms of motivational theory, they can do this in terms of altering 'motivational thresholds' (i.e. the motivational strength required to activate a particular behaviour). In terms of neurophysiology, genes could influence the numbers, distribution and responsiveness of specific receptors to circulating hormones and neurotransmitters, and hence influence behaviour. Given experience, environmental cues will then "shape" and sensitise neuronal pathways according to specific environmental conditions. Thus, the farrowing sow's individual predisposition interacts with the restrictive farrowing environment such that individuals will respond differently to the same environment.

Studies in rats have shown that chronic stress can lead to permanent changes in different receptor densities in the central nervous system, i.e. receptor up- and down-regulation. For example, after a period of chronic stress the pituitary adrenal system can become hyper-sensitive such that adrenocorticotrophic hormone (ACTH) is secreted in increased quantities when the animal is exposed to new stressors (Sakellaris and Vernikos-Danellis, 1975). A possible mechanism suggested for this phenomena is increased anterior pituitary sensitivity to vasopressin, which potentiates the corticotrophin releasing hormone (CRH) induced adrenocorticotrophin hormone secretion (ACTH) (Hashimoto *et al.*, 1988).

Sows kept in farrowing crates appear capable of adapting their endocrine systems during the course of one parity. Acute exposure to behavioural restriction during parturition results in an opioid mediated inhibition of oxytocin secretion, prolonging parturition (rats - Leng *et al.*, 1988; pigs - Lawrence *et al.*, 1992; but see Gilbert *et al.*, 1997). Whilst chronic exposure to behavioural restriction in farrowing crates (from 5 days prior to parturition) causes a long-term elevation of cortisol, with concurrent elevated hypothalamic opioid tone (Laatikainen, 1991; Lawrence *et al.*, 1994; 1997). It has been suggested that this causes a degree of local opioid tolerance, decreasing the sensitivity of the oxytocin system to opioid inhibition (Douglas *et al.*, 1993; Lawrence *et al.*, 1995). Thus, when afferent stimulation arrives at the start of parturition (e.g. vagino-cervical dilation), and the original stressor is removed (i.e. no longer motivated to nest-build), oxytocin comes flooding out of the posterior pituitary (Lawrence *et al.*, 1995; Gilbert *et al.*, 1996). Thus, Lawrence *et al.* (1995) found that gilts in crates have higher levels of circulating oxytocin at the start of parturition, and a initial high rate of piglet expulsion, than gilts in pens.

Physiological adaptation within parity has also been demonstrated in pseudopregnant gilts induced to nest-build by prostaglandin $F_{2\alpha}$ (Boulton *et al.*, 1997a, 1997b). The gilts used in this study were either transferred to farrowing crates without straw or left in their straw pens. Gilts transferred to the farrowing crate had lower levels of prolactin and progesterone four days after the move than gilts left in their straw pens (Boulton *et al.*, 1997b). After this period, levels of progesterone and prolactin were the same for gilts in both environments suggesting physiological adaptation in the crated gilts (Boulton *et al.*, 1997b). On the fifth day, all gilts were injected with prostaglandin $F_{2\alpha}$. The injection had no effect on prolactin levels but in crated gilts levels of progesterone rose sharply, indicating sensitisation of this physiological system (Boulton *et al.*, 1997b). Moreover the authors presented a graph depicting higher oxytocin levels in the crated gilts the day after prostaglandin injection, whereas before the injection farrowing environment had no effect on oxytocin levels (Boulton *et al.*, 1997b - fig. 1a, p. 1081). This is consistent with the hypersecretion of oxytocin at the start of parturition found by Lawrence *et al.* (1995) in crated gilts.

Adaptation to farrowing crate conditions can also be seen by comparing the behavioural and physiological responses over subsequent parities. As mentioned above, levels of cortisol pre-farrowing suggest that behavioural restriction in the farrowing crate during nesting results in an aversive psychological state (Lawrence *et al.*, 1994). This physiological response to the crate is more pronounced in first parity gilts than second parity sows (Lawrence *et al.*, 1994; Jarvis *et al.*, 2001, in press), which may reflect a change in how aversive the sow perceives the farrowing crate to be.

Sows' preference for type of farrowing crate depends on parity, with preference for a partially-enclosed crate (solid-sided) found only in sows in their first three parities and not in older sows (Phillips *et al.*, 1991). This suggests that a sows perception of the best type of farrowing crate to give birth in can change as a result of experience of crates. Similarly, the behaviour of sows of parity four or greater were less affected by the presence of sawdust in the crate than sows in their first three parities (Cronin *et al.*, 1993). Therefore, older sows have a lowered responsiveness to differences in their environment than younger sows, which may be a consequence of experience of nest-building in crates.

Aims of the Thesis

1. To describe the behaviour of sows pre-farrowing, during parturition and post-farrowing. In order to (A) identify consistency and change over parities, describing breed differences and exploring the influence of straw in the farrowing crate. (B) Identify behaviours that appear to have genetic influences and look for evidence of behavioural adaptation to farrowing crates between parities one and two (Chapters 3, 4).

2. To identify the relationships between, and non-behavioural causes of, different types of piglet mortality (Chapter 5).

3. The identification of the behavioural characteristics associated with piglet savaging and piglet crushing sows in order to move towards an understanding of what constitutes adaptive, good maternal behaviour (Chapters 6, 7). Identify which of these behavioural characteristics show evidence of genetic influences (Chapters 3, 4).

These aims are achieved by studying the behaviour and piglet mortality records of a large sample of sows and gilts from four different genotypes. Data collection took place over approximately two years and first parity sows were observed again as their second parity where possible. This allowed the identification of consistency and change in behavioural expression over the first two parities. Consistent behaviours represent stable maternal traits of the sow. The comparison of different breeds indicated whether breed-dependent influences were affecting the behavioural and piglet mortality data. Stable breed differences indicate a possible genetic basis to a trait. Additionally, the presence or absence of straw in the farrowing crate was incorporated into the experimental design. Straw is known to influence at least one aspect of maternal behaviour, nest building, so it was thought that other aspects of maternal behaviour might also be influenced by straw, which may have consequential effects on piglet mortality.

CHAPTER 2:

GENERAL METHODS

Introduction

The results contained within chapters three, four, five and six, were a consequence of one, longitudinal experiment, the details of which are described in this chapter.

In any experiment it is essential to standardise and control external sources of variation not relevant to the experimental design. When this can not be done, an attempt must be made to identify and measure all potential sources of variation so that their effects might be quantified.

In breed studies like this, the environment and early life experiences must be standardised across all breeds so that inferences can be made about breed-specific genetic influences. Complex gene by environmental interactions may exist whereby breed differences for a particular trait only develop as a result of the animal experiencing a particular environment. Therefore breed differences, even when all breeds are reared in the same environment, can be a very crude indication of genetic influences on a measured trait.

Subjects and husbandry

The Farm

All the pigs used in this study were housed at Cotswold Research and Development Unit, Wye, Kent, which is run in alliance with Imperial College, University of London. The unit houses many different genotypes including Meishan, 50% Meishan

composite, Pietrain and Duroc as well as standard commercial Large White × Landrace type hybrid gilts and sows.

Housing and Rearing

Weaned piglets are taken from the farrowing house at an average of 26 days old and minimum weight of 6kg and put in single-sex groups of about 30-35 in kennels. In the kennels the piglets are provided with straw and have *ad libitum* access food and water. At this stage piglets are weaned into sex specific pens, although where necessary genotypes are mixed.

At approximately six months of age, gilts are moved to straw yards where they are kept in groups of around ten. At this point, gilts are separated into their genotype group. Gilts are first served at approximately 230 days (or 7.5 months) of age, but slight breed differences exist here. Sows are housed in larger straw yards to the gilts and in groups of up to eight. Sows in the same yard tend to be of the same genotype but this is not always the case. During service, sows are taken from their straw yard to a service pen in the same building. Boars are present in adjacent pens. All services were to one boar only. The majority of services (approximately 80%) were artificial insemination, the remainder were via natural methods. All sows were batch farrowed such that at any one time only one genotype is being served, another farrowed. A target of 40 farrowings in one 4-week period is adhered to. This requires a total of 50 sows serves in each 4-week period. These services are split into weekly targets of 10 per week for the first three weeks and 20 for the last week. The exception to this is during 'crossover' week at the end and beginning of batches where 2 genotypes may be served in the same week. Although most sows would usually farrow approximately 2.2 times a year this system of batch farrowing requires some sows to be kept for one or more heat cycle to ensure service and farrowing at the correct time, so actual farrowings per year are somewhat less than 2.2.

At approximately five days prior to the expected farrowing date, gilts and sows were taken from their straw yard group gestation pens to the farrowing house. There were

two designs of farrowing house on the Wye site, known as the 'new' and 'old' farrowing houses, with different styles of farrowing crate (see Figure 2.1). The distance the sow must walk from the gestation pen to the farrowing crate varied from 20 to 150 m, depending on which farrowing house was used (the old houses were further away) but was not dependent on breed, parity, treatment or season. There were 39 crates in the old farrowing house and 16 crates in the new farrowing house. There were two types of crate, which differed in the space available to the piglets in relation to the position of the sow (see Figure 2.1) but not in the amount of space for the sow.

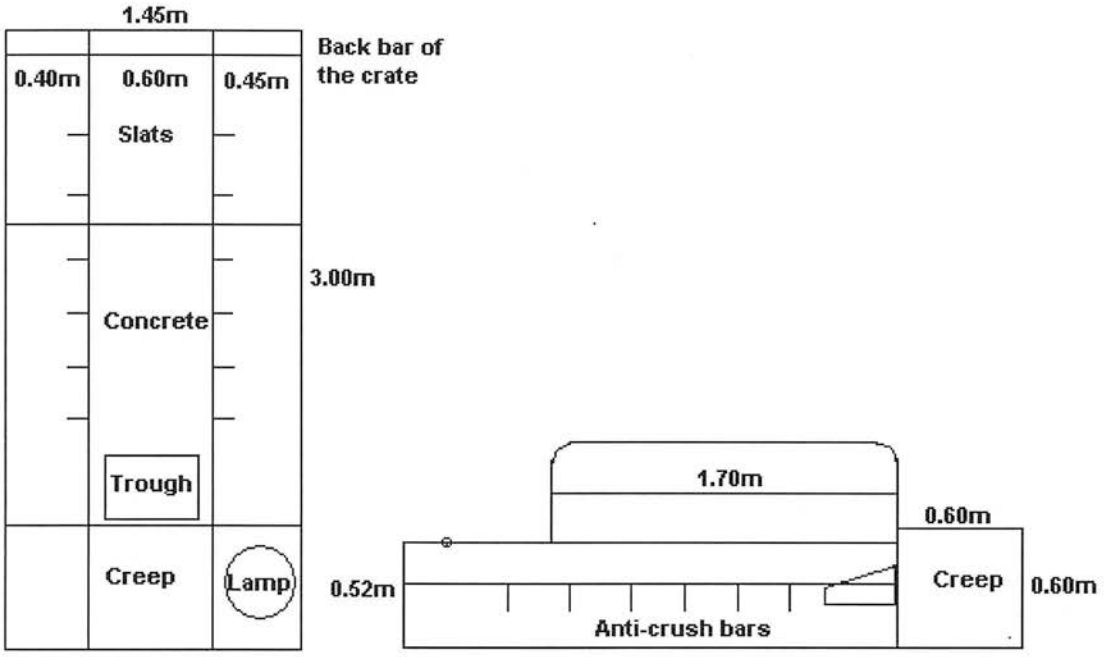
The air temperature in the farrowing house was monitored. The farrowing houses have ventilation fans which help control the temperature (and dust levels) in the building; whilst the majority of the light in the farrowing houses is artificial. Litter differences due to old versus new farrowing houses were accounted for by including farrowing house as a factor in subsequent analyses.

In this study half of all the sows and gilts had access to 2 kg of straw in the farrowing crate. The other half of the subjects in this study farrowed in crates without straw. The sows remained in their farrowing crates until their piglets were weaned at 4-5 weeks.

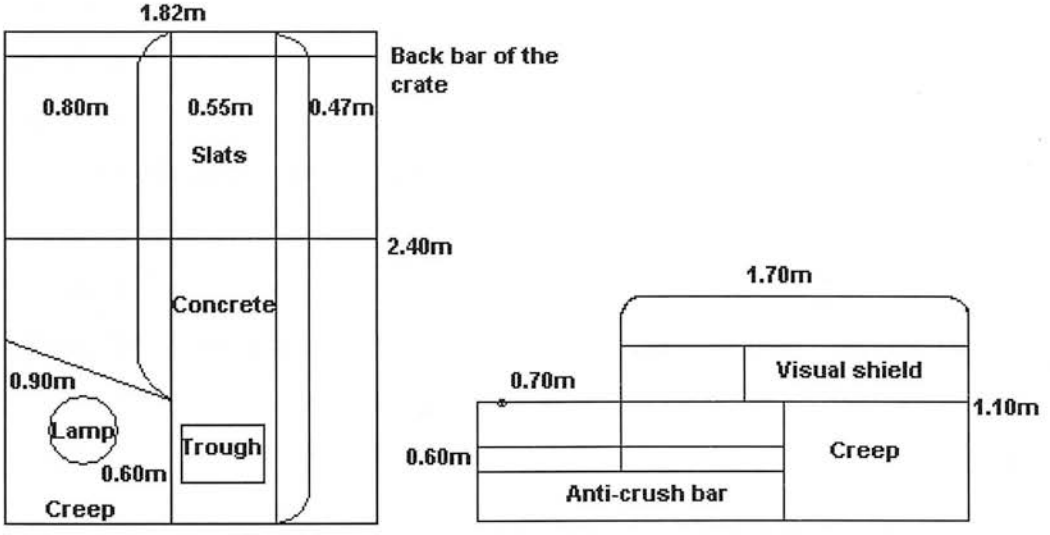
Sows were fed twice a day, once at 0800 hrs and again at 1600 hrs except during the first week post-farrowing when sows were given their full daily ration at approximately 0800 hrs.

Figure 2.1: Scale drawings of (a) the old style of farrowing crate and (b) the new style of farrowing crate

(a) Old Crate



(b) New crate



The Breeds

Four breeds were used in this study:

1. Pure-bred Meishan (M)
2. Pure-bred Duroc (D)
3. 50% Meishan, 50% Landrace synthetic line (breeding pure) (ML)
4. 75% Landrace, 25% Duroc synthetic line (breeding pure) (LD)

All breeds were reared, housed and treated identically.

The pure-bred Meishans are a black Chinese breed maintained as a small population of about 15 sows and 15 boars. The Meishan sows are kept until the end of their first farrowing when they are culled and replaced by a sample of their offspring, with the aim of maintaining the variability present in this genetic resource. The Meishan breed is a breed that has remained unselected in the UK. The process of domestication, in Asia, which has resulted in this breed remains obscure. Recent research which looked at Cytochrome B variants and mitochondrial DNA D-loop sequences of various modern breeds has pointed to the Asian and the European wild boars as being distinct at the sub-species level (Leif Andersson, pers. comm., Pig Breeders Round Table, 1999). The Meishan breed was chosen for this study of maternal behaviour because previous research has identified this breed as having superior maternal qualities to the European breeds (see Chapter 1).

The pure-bred Duroc is a breed maintained at a higher population level (around 40 sows) on the Wye unit and are usually kept for three parities. The original red colour of the Duroc breed has been bred out of the Duroc population at Wye to produce a 'white Duroc'. This was achieved by crossing Duroc with Large White, and back-crossing the white offspring with the original Duroc population for six generations, selecting only white offspring. The resultant population, which is now mated *inter se*, contains, on average, 97% Duroc genes and 3% Large White genes. Since only a proportion of the Duroc progeny are re-bred from it is possible that the process of breeding out the red coloration may have also bred out other traits associated with

the original Durocs. However, breeding out the red colouration was deemed necessary to satisfy the European consumers requirements for pig meat. The Duroc herd at Wye has undergone BLUP selection for lean growth for several generations. This breed was chosen for the purpose of this study because the lack of any selection for maternal traits, principally litter size, may have resulted in a breed with different maternal quality to the other selected breeds. One possibility is that the smaller litter size in the Duroc has meant that Duroc piglets receive, on average, more maternal investment per head than piglets born into larger litters, which may improve piglet survival. Alternatively, overall maternal quality may have improved along with litter size amongst the breeds selected for litter size.

The 50% Meishan, 50% Landrace (ML) breed is maintained at a population level of around 60 sows at the Wye unit. This line has been selected for 9 years using BLUP for a combination of reproductive performance and lean growth with approximately 70% of the selection emphasis directed at reproduction.

The 75% Landrace, 25% Duroc composite breed (LD) is maintained at a population size of around 20 sows. This line has been selected for 15 years using BLUP for a combination of reproductive performance and lean growth with approximately 70% of the selection emphasis directed at reproduction. Only white offspring are re-bred from, which may have the effect of reducing the proportion of Duroc genes in this breed. This breed is the female component of Cotswolds' commercial gilt lines.

The batch farrowing system employed at Wye created the potential problem of breed effects being confounded by season. However, for some breeds data was collected over all four seasons making it possible, when time of year was divided into seasons, to estimate the influence of season on sow behaviour and piglet mortality and separate season from effects of breed. The number of farrowings per breed and per season collected during this study is presented in Table 2.2.

Table 2.2: The distribution of farrowings from each breed over the four seasons. Sample sizes for results Chapters 3, 4, 6 and 7 are shown, with the sample size for results Chapter 5 displayed in brackets.

	Winter (Dec-Feb)	**Spring (Mar-May)**	**Summer (Jun-Aug)**	**Autumn (Sep-Nov)**
Duroc	6 (8)	27 (45)	4 (5)	18 (23)
Landrace-Duroc	0 (0)	8 (11)	0 (0)	8 (8)
Meishan-Landrace	20 (23)	14 (23)	24 (27)	13 (17)
Meishan	6 (6)	11 (14)	0 (0)	0 (0)

The number of farrowings for each breed farrowing in each season was further sub-divided into parity and treatment (for a description of treatment, see below). During the analyses of Chapters 3, 4, 6,and 7 interaction terms between breed, season, parity and treatment were included in the models describing the data.

Experimental Design

The experimental design took the form of a breed by treatment by parity factorial experiment. Four breeds were studied (see above for descriptions of the breeds). Differing population sizes between the breeds, the management decision to cull one of the breeds after its first parity, and the natural drop-out rate between parities one and two resulted in an unbalanced design. Three of the breeds, Duroc, Landrace-Duroc and Meishan-Landrace, were observed over parities one and two, whilst the fourth breed, Meishan, was observed during parity one only. In the first three breeds, the same individuals were observed over both parities in order to measure consistency and change in behaviour over the two parities. Gilts were randomly assigned a treatment, which was the presence or absence of straw in the farrowing crate. Treatment allocation in the second parity was dependent on the treatment allocation in the first parity. Half of all sows that received straw in parity one,

continued to receive straw in parity two, whilst the other half were not given straw. Similarly, half of all sows that did not receive straw in parity one, did not receive straw in parity two, whilst the other half did receive straw (see Table 2.3). This partial cross-over design allowed for: a) the identification of straw effects independent of sow effects; b) the identification of potential effects of having a consistent environment, in relation to whether straw was present in the crate, over the two parities.

The parity, breed and treatment sample sizes obtained using this design are summarised in Tables 2.3 and 2.4.

Table 2.3: Treatments were randomly allocated to produce four treatment groups for the three breeds that were observed over two parities. Sample sizes are shown for the Duroc and Meishan-Landrace breeds for each of the four treatment groups. In Landrace-Duroc, the sample size (see Table 2.4) was too small to sub-divide into these four treatment groups.

Treatment Group	Parity 1	Parity 2	Duroc	Meishan-Landrace
SS	Straw	Straw	8	11
SN	Straw	No straw	5	11
NS	No straw	Straw	6	7
NN	No straw	No straw	5	8

Table 2.4: Experimental sample sizes for breed, treatment and parity comparisons. Numbers that are presented further to the right are sub-divisions of the previous number to the left (e.g. 96 parity one gilts, of which 31 are Duroc, 11 are Landrace-Duroc, 37 are Meishan-Landrace and 17 are Meishan). Individual sows were observed over two parities except for the Meishan gilts, which were all culled after parity one.

Group	Sample Size	Group	Sample Size
Parity 1	96	**Parity 2**	63
Duroc	**31**	**Duroc**	**24**
Straw	18	Straw	14
No straw	13	No straw	10
Landrace-Duroc	**11**	**Landrace-Duroc**	**5**
Straw	7	Straw	1
No straw	4	No straw	4
Meishan-Landrace	**37**	**Meishan-Landrace**	**34**
Straw	19	Straw	19
No straw	18	No straw	15
Meishan	**17**		
Straw	9		
No straw	8		
Straw	**53**	**Straw**	**34**
No Straw	**43**	**No Straw**	**29**

Measurements

Breeding Record

The identity of each gilt's parents (sire and dam) and the gilt's date of birth were obtained from archived breeding records. The identity of the service boar used on the dam, serving method used (Artificial Insemination or natural) and date of service was

obtained from the service records available on site. The date of service was used to calculate the expected farrowing date, on average 114 days later for ML, LD and D gilts and sows and 112 days for Meishan gilts.

When selecting gilts to be observed, care was taken to maximise the spread of sire families represented in the experiment. This was done so that inferences about the on-farm population of that breed could be made from the breed differences observed.

Farrowing Data

The following information for each sow or gilt, was collected at each farrowing:

1. Sow identification number, breed and parity
2. Ease of movement (graded 1 to 5, see below) during the move from group pen to crate
3. Date and time put in crate
4. Farrowing date
5. The crate and house in which the sow or gilt farrowed
6. Whether a radio was used as background noise during farrowing
7. Number of piglets born alive
8. Number of pre-term mummies born (under-developed aborted foetuses)
9. Number of full-term still-births
10. Date of each pre-weaning mortality, with the cause where known
11. If drugs were used on the sow or gilt, the type of drug, date, time and quantity of each dose
12. If cross-fostering occurred, the number fostered on or off, the dates, the foster sow used or the sow from which the piglets came
13. Number, date of weaning and weight of each piglet weaned
14. Maximum and minimum daily temperature of the farrowing house

When scoring ease of movement from group pen to crate, the farm staff were given the following guidelines:

1 = sow moves calmly from yard to farrowing crate, requires very little persuasion to move in the desired direction.

2 = sow is moved in a controlled way although sometimes requiring persuasion and some force to keep her going in the right direction.

3 = sow is more difficult to move and occasionally strains against the stockperson trying to move her; however, does not attempt to bolt away or resist movement more than 3 times.

4 = sow reluctant to move but does so after much coaxing; may attempt to bolt away or resist movement but does not do so continuously.

5 = sow makes every attempt to resist movement and requires considerable force to keep her under control and moving in the desired direction.

The ease of movement score was developed from a movement scoring method used by Ahlstrom (1997), during attempts to develop a method of identifying different maternal styles. In the Ahlstrom (1997) study, there were no correlations between the sow or gilts movement score prior to parturition and her behaviour towards her piglets during and immediately after parturition. However, this could have been due to the small sample sizes used.

Guidelines were followed when attributing the cause of death to a piglet mortality. The definitions used for each piglet mortality are detailed in Table 2.5. Mortalities that occurred during the first 24 hours following the birth of the first piglet were verified using the video record. At the time of farrowing, the farm staff made no attempt to distinguish between intra-partum still-births, pre-partum still-births and piglets dying soon after birth. However, some of the piglets that died soon after birth originally classified as still-births could be re-classified from the video record with their ultimate cause of death. There was no attempt to distinguish between the crushing mortalities of healthy piglets from the crushing mortalities of piglets weakened by either sow aggression, pre-longed parturition or low food intake. This would have required greater time input from the farm staff, a video record with more

detailed resolution and the identification of individual piglets from the video. These were constraints on the data collected.

Video verification of the piglet mortalities noted by the farm staff was carried out on the 159 sow farrowings which were the subject of Chapters 3, 4, 6 and 7. In Chapter 5, an additional 51 farrowings were included in the piglet mortality analysis. Video verification was not possible for 51 of the 210 farrowings analysed in Chapter 5.

Table 2.5: The definitions used for different causes of piglet mortality.

Cause of Death	**Operational definition**
Still-birth	Fully developed piglets born dead or dying within the first few minutes following birth. Intra-partum still-births were not distinguished from fully developed gestational still-births.
Crushed	Piglets found dead showing signs of being laid on by the sow; e.g. squashed rib cage, red spots on the nose indicating blood having been forced towards the head.
Savaged	Piglets found dead with large bite marks associated with the sows mouth size and not from sibling fights.
Starved	Piglets found dead after several days of noticing that the same piglet was failing to compete successfully for a teat. Small piglets with poor weight gain.
Congenital Abnormality	Piglets born with genetic defects which seriously reduced their chance of survival. Examples included: splayed legs, heart problems, blind anus and joint illness. These piglets either die naturally or are culled.
Non-viable	Small, weak piglets unlikely to survive. Most of these are culled before they would succumb naturally.
Other (unknown or unspecified)	This category is reserved for deaths where the cause is either unknown or unspecified.

Video Record

The sows behaviour was recorded from Panasonic colour closed-circuit cameras positioned to the rear of the crate and looked down on the sow from behind. In the old farrowing house the cameras were positioned 1.46 m to the rear of the crate and 1.90 m off the ground; in the new farrowing house the cameras were positioned 1.00 m to the rear of the crate and 1.90 m off the ground. The camera angle was such that the rear of the sow or gilt was at the bottom of the picture and its head was at the top of the picture. Video recording started three days prior to the expected farrowing date and continued until three days post-farrowing.

Eight cameras were linked to a Panasonic WV-CM 146 Colour Monitor. This took an image from each camera input sequentially and recorded it on to Fuji Super SHG 180 tapes via a Panasonic AG 6024 time-lapse video recorder. The video recorder operated in 24-hour time-lapse mode, giving a resolution of fifty frames per nine seconds divided between the number of cameras being operated. When all eight cameras were being used, an image was recorded from each camera every 1.44 seconds. When fewer cameras are used, the number of frames per second per camera was higher. A Vertical Interval Time Code (VITC) generator box added a time code to the video signal before the combined signal was recorded onto tape.

The analysis of the video tapes took place at a later date. Playback was via an AG 6124 time-lapse video recorder onto a Panasonic WV-CM 146 Colour Monitor, with a video signal going to a time code reader board installed on a computer. Tapes were analysed mostly in 3-hour mode, although during periods of high activity a 12 or 24 hour time mode was used. The Observer Video Analysis software (Noldus Information Technology b.v., Wageningen, 1997) was used throughout to code the behavioural observations.

The behavioural categories observed and the definitions used are presented in two ethograms found in Tables 2.6 and 2.7.

Table 2.6: The Pre-Farrowing Ethogram

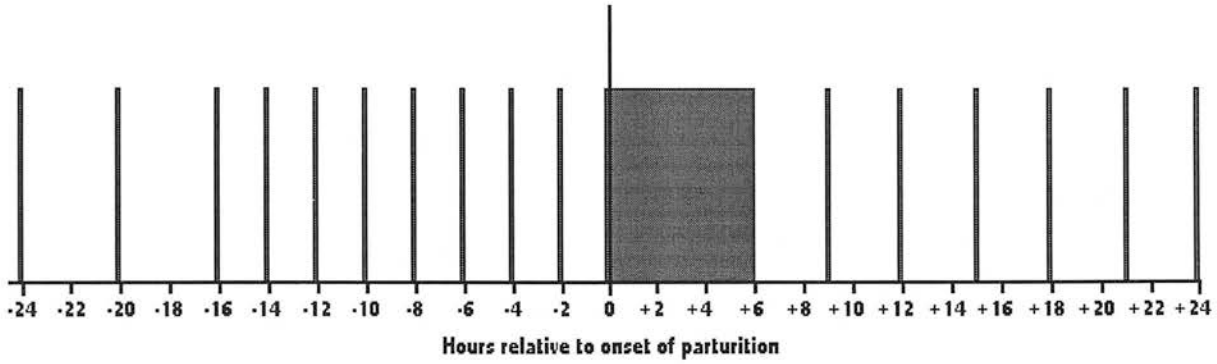
CLASS	ELEMENT	EVENT/ STATE	DESCRIPTION
Posture	Stand	S	Sow is upright with weight on all four feet and legs extended.
	Back-up	S	Sow is upright, weight on all four feet, legs extended; with rear of sow pushed back against the rear of the crate.
	Sit	S	Front end of sow is raised, back end is in contact with floor.
	Kneel	S	Back end of sow is raised, front end is in contact with floor. Tends to be a transitory posture during lying down, or used when the sow tries to reach something under the trough or bars.
	L ventral	S	Sow is lying with sternum in contact with the floor, udder not visible, neither shoulder in contact with floor. Spine is left of centre as viewed from behind.
	C ventral	S	Sow is lying with sternum in contact with the floor, udder not visible, neither shoulder in contact with floor. Spine is in a central line, leaning neither to the left or right.
	R ventral	S	Sow is lying with sternum in contact with the floor, udder not visible, neither shoulder in contact with floor. Spine is right of centre as viewed from behind..
	L lateral	S	Sow is lying with left shoulder in contact with the floor and legs extended. Udder is visible.
	R lateral	S	Sow is lying with right shoulder in contact with the floor and legs extended. Udder is visible.
	Other posture	S	Any other posture not described above.
Behaviour	Head movement	S	Sow is either standing, sitting or laying and head moves from side to side. Sow looks around but is not interacting with her environment in any other way.
	Inactive	S	Sow is not engaged in any activity that involves movement of the body or head.
	Trough	S	Sow has head in trough and is either eating or drinking. Usually a calmer activity than fixture-directed behaviour around the trough.
	Fixtures	S	Sow manipulates/mouths bars, trough or other fixtures.
	Straw	S	Sow mouths, paws, roots, or otherwise manipulates straw.
	Floor	S	Rooting and pawing movements directed towards the floor.
	Slide	E	Sow kneels and pushes her head underneath the trough.
	Lift	E	Sow climbs the crate bars or trough and pushes head through the crate bars.
	Step	E	Whilst standing, the sow raises a foot and replaces it in a different position. If a sow appears to have moved between subsequent video frames, one step event is logged.

Table 2.7: The Parturition and Post-Farrowing Ethogram.

CLASS	ELEMENT	EVENT/ STATE	DESCRIPTION
Posture			***As for the pre-farrowing ethogram.***
Behaviour			***As for the pre-farrowing ethogram, and including:***
	Birth	E	A piglet emerges from the birth canal. A birth event is recorded when the whole piglet is expelled. In situations when the sows' vulva is not visible, the birth event is assumed to follow the last contraction event preceding the first appearance of the piglet on the screen. (For this reason, still-births may not always be logged.)
	Look at	S	Sow looks specifically at piglets. Sow follows the movement of piglet with her head.
	Touch	E	Sow touches area of piglets' body, other than piglets' nose, with her nose.
	Nose	E	Reciprocal nose to nose contact between sow and piglet.
	Root piglet	E	Sow pushes piglet away using the bridge of her snout.
	Bite	E	Sow is seen with mouth around piglet. Definite aggressive act.
	Snap	E	Attempted bite. Sows head moves rapidly towards a piglet with mouth open. Piglet does not end up being in sows' mouth.
	Savage	S	Prolonged act of aggression towards piglet(s), involving biting, picking up a piglet in the mouth and the sow shaking her head.
	No response	E	Piglet is within one bodylength of sows' mouth, in the facial half of the sows' head - an imaginary arc from the ears to lower neck. Event is scored again only if the piglet moves away and then approaches again, or if the piglet climbs on to the sows head. (Scored only once if the piglet just remains within the vicinity of the sows head.)
	Crush no response	E	Sow lays on top of, or steps on, a piglet and sow fails to react by moving off the laid on piglet within 1 minute of the piglet first being trapped.
	Crush response	E	Sow lays on top of, or steps on, a piglet but moves off the laid on piglet within one minute of the piglet first being trapped.
	Near miss	E	Sow begins to lie down whilst piglets are still underneath her. However, a piglet does not end up being crushed mostly due to the piglet moving away at the last second.

Sampling Protocol

Figure 2.2: Graphical representation of the behaviour sampling protocol. The solid bars indicate the times when continuous behavioural observation of the sow takes place. The solid bar between 0 and +6 hours indicates continuous sampling for that 6-hour period.



Pre-farrowing

Pre-farrowing behaviour was sampled continuously for 10 minutes prior to each of the following points in time relative to the birth of the first piglet (BFP, time 0):

-24, -20, -16, -14, -12, -10, -8, -6, -4, -2, 0

These sample points were concentrated around the time when nest-building behaviour is thought to occur, i.e. within 16 hours before the onset of parturition (Jensen, 1993; Jarvis *et al.*, 1997). (See Figure 2.2 for a summary.)

Post-farrowing

Post-farrowing sow or gilt behaviour was sampled continuously for six hours following the birth of the first piglet. Thereafter, ten minute samples were taken every three hours until 24 hours post-farrowing (at 8:50, 11:50, 14:50, 17:50, 20:50 and 23:50 hours (see Figure 2.2 for summary).

During periods of human intervention, recording of the sow and piglets behaviour was stopped. Behavioural recording stopped the moment someone entered the farrowing crate or surrounding area and resumed five minutes after the person had left. Similarly, if the sow's piglets were locked in the creep, behavioural recording stopped until five minutes after the piglets were released.

Piglet scan samples, of the behaviour and location of the litter as a whole, were taken every five minutes to coincide with sow observations. These scan samples provided an indication of how piglets partitioned their time. At each scan sample the number of piglets in each of eight categories (see Table 2.8) was recorded. When a piglet was born dead, its presence was recorded once at the scan sample following birth but not for subsequent scan samples. Similarly, when a live-born piglet died, its position was only recorded once after it had died but not for subsequent scan samples.

Table 2.8: The eight scan sample categories used to classify piglet behaviour and location.

Scan Sample Category	Description
Vulva:	Piglets within one bodylength of the sows' vulva
Creep:	Piglets in creep area
Udder active:	Piglets active at udder, suckling or massaging a teat
Udder inactive:	Piglets inactive at udder
Sows' head:	Piglets within one piglet bodylength of the sows' head
Under sow:	Piglets underneath the body of the sow
Other active:	Piglets active but not at the udder, sows' head, vulva or in the creep
Other inactive:	Piglets inactive but not at the udder, sows' head, vulva or in the creep

Sow size

The video record was also used to estimate sow size. This was deemed important for two reasons:

(a) To account for breed differences in size, which might invoke a systematic bias when interpreting breed differences in the behaviour of sows in confined spaces. Sow size was included in subsequent analyses of behaviour and piglet mortality. Measuring the size of the sow was more practical than standardising the relative amount of space each sow had in the farrowing crate.

(b) Previous research (e.g. van der Steen *et al.*, 1988) has identified sow weight after parturition as being a predictor of degree of restlessness and risk of savaging. It was thought that sow size as measured from the cameras' perspective might be a good enough estimate of sow weight to test this finding.

The measurement of sow size taken from the video screen were length, from the shoulder to the base of the tail, whilst the sow was standing with a straight back and with her rump touching the back of the crate. These measurements were made with an error of about 5% for length (i.e. 100 +/- 5 mm). Sow length, as measured from the video screen was converted to approximate real-life length using the known crate dimensions and relating these to their lengths on the video screen. Measurements of sow size were taken during the pre-farrowing period when it was easier to find instances of the sow standing.

Summarising the behaviour data

Behavioural data files obtained by using continuous focal animal recording methods can be summarised in many ways, the nature of these data summaries being critical to the outcome of any subsequent statistical analysis made on them.

The first consideration was the length of the time sample for which means and counts should be taken for comparison between sows. These sample lengths must be appropriate to the biological phenomena being described, for example data that can answer questions related to the progress of parturition must have sample lengths considerably shorter than the mean length of parturition.

The following is a summary of how the behavioural data was summarised and extracted from the observational data files.

a) Posture changes

The frequencies of different types of posture changes were extracted using Lag Sequential Analyses (Noldus Information Technology b.v., Wageningen, 1997). There were nine different postures, as defined in the ethogram above, giving 72 possible posture changes, some of which are rarely if ever seen. This number was reduced to 12 types of posture changes which previous research had shown to be important in predicting risk of crushing (Edwards *et al.*, 1986; Weary *et al.*, 1997a; Wechsler and Hegglin, 1997). Table 2.9 shows an example of one posture transition matrix and a summary of the posture changes obtained from such a transition matrix.

Table 2.9: Transition matrix produced by a State Lag Sequential Analysis of posture changes. Criterion events (starting posture) are found in the first column and target events (finishing posture) on the top row of subsequent columns. These are the posture states described in the pre-farrowing ethogram (table 2.6). The types of posture changes obtained from such a matrix are summarised below.

	Stand	Sit	Kneel	Right lateral lie	Left lateral lie	Central ventral lie	Right ventral lie	Left ventral lie	Back-up
Stand		0	2 ∇	**0**	**0**	0	0	0	0
Sit	2 ♦		0	**2**	**0**	0	6	0	0
Kneel	0 #	0		**0**	**0**	0	1	1	0
Right lateral lie	**0**	**2**	0		**0** *	**1**	**2**	**0** *	0
Left lateral lie	**0**	**0**	0	**0** *		**0**	**0** *	**1**	0
Central ventral lie	**0**	**0**	0	**1**	**0**		**0**	**0**	0
Right ventral lie	**0**	**6**	0	**2**	**0** *	**0**		**1** *	0
Left ventral lie	**0**	**2**	0	**0** *	**1**	**0**	**0** *		0
Back-up	0	0	0	**0**	**0**	0	0	0	

Standing and sitting up	**Lying down**	**Changing lying postures**
Lie – sit **violet bold**	Kneel – lie ▬	Lie 1 – lie 2 **red bold**
Lie – stand **blue bold**	Stand – lie ▬	Roll (Ventral lie – lateral lie) **red bold underlined**
Sit – stand ♦	Sit – lie ▬	Swap sides * (left to right, right to left)
Kneel – stand # (aborted lying down)	Flop (Stand, backup, sit or kneel – lateral lie) **green bold**	

Counts of types of posture changes were made for each successive one hour interval during the six hour observation period following the onset of parturition (refer to Figure 2.2). This hourly interval was chosen on the basis that posture changes are relatively infrequent in most farrowing sows and so shorter intervals would have produced variables with too many zero values for analyses purposes.

The six 10 minute post-farrowing samples, at 9, 12, 15, 18, 21 and 24 hours following the onset of parturition, were combined to form a seventh hour that could be compared with the previous six observation hours following the onset of parturition.

(b) Percentage Time Spent

Samples from the pre-farrowing period, of which there were eleven 10-minute samples, were grouped into four blocks for behavioural summary. Block one contained the -24 and -20 hour samples and represented 20 minutes of information spread over six hours. The next three blocks containing three 10-minute samples, represented 30 minutes of information spread over six hours. Block two was made up of samples from the -16, -14 and -12 hour samples; block three from the -10, -8 and -6 hour samples; and block four from the -4, -2 and 0 hour samples. Grouping the pre-farrowing samples this way acted to average out extreme values, for example if the sow or gilt had just been given food she will probably spend the entire sample feeding, whilst still retaining some information on changes over time during the pre-farrowing period.

Percentage time spent was calculated for all postures and all behaviours that were states (see the ethograms in Tables 2.6 and 2.7). These were calculated for the four pre-farrowing time blocks (30 minutes) referred to above, and for each successive 30 minute unit of time following the birth of the first piglet (BFP). This divided up the six hour observation period following BFP into twelve time intervals and created two

further time intervals representing the observations at 9, 12 and 15 hours post-BFP and the observations at 18, 21 and 24 hours post-BFP.

For some analyses these 30 minute post-BFP time intervals were collapsed to form one hour time samples (e.g. Chapter 6) or one measurement for the entire seven hours of observation post-BFP (e.g. Chapter 7).

(c) Frequency of Occurrence

Frequencies or counts were collected for all behavioural events (e.g. births, bites, no responses – see ethograms, Tables 2.6 and 2.7). As before, the time interval chosen was 30 minutes.

Frequencies measured during the first pre-farrowing time block (-24, -20 hours) were multiplied by 1.5 in order to make them comparable to the frequencies measured during the other three time blocks.

(d) Mean Duration

The pre-farrowing substrate-directed behaviours (straw, floor and fixture-directed behaviour) were also described in terms of mean duration of each occurrence. Mean duration was defined as the total time spent doing a particular behaviour divided by the number of times the behaviour was initiated during a particular sample. This is a crude measure of bout length that makes no assumption as to when a bout begins or finishes (i.e. not a log survivorship analysis).

Summary and Conclusions

1. The experimental design was based around a breed by treatment by parity factorial design, where treatment was the presence or absence of straw in the farrowing crate and individual gilts were observed over two parities. Differing population sizes between the breeds, the management decision to cull one of the breeds after its first parity, and the natural drop-out rate between parities one and two resulted in an unbalanced design.
2. Four breeds were studied. These were two pure-breds, Duroc and Meishan, and two synthetic breeds, Landrace-Duroc and Meishan-Landrace. All breeds were reared, housed and treated in the same way, increasing the likelihood that any breed differences observed would represent genetic influences.
3. A partial cross-over design was applied to the allocation of treatment over the two parities. In parity one, gilts were randomly assigned either straw or no straw in the farrowing crate. In parity two, half of the sows that experienced straw during the previous farrowing, received straw for their second farrowing, whilst the other half did not receive straw. Similarly, half of the sows that experienced not having straw in the previous farrowing, did not have straw for their second farrowing, whilst the other half received straw. This allowed for straw effects to be identified independent of sow effects, whilst also providing information on the effect of consistency of environment over successive farrowings.
4. Detailed farrowing records were filled in by farm staff in an attempt to identify variation between litters not due to breed, parity or treatment. These records contained information about cross-fostering practices, whether drugs were given to the sow or gilt and whether noise from a radio was a feature of the farrowing house.
5. The cause of each piglet mortality was recorded using a list of definitions describing the external appearance of the dead piglet. Mortalities that happened during the first 24 hours following birth were verified from video observation. There was no attempt to distinguish crushing mortalities of healthy piglets from the crushing mortalities of weakened piglets, because this was deemed too subjective when only observation can be used to assess cause of death. There was

also no attempt to distinguish between intra-partum still-births, pre-partum still-births and piglets dying soon after birth, again for practical reasons. Although video observation was used to re-classify some of the piglets dying soon after birth if they were crushed or savaged.

6. The ease with which a sow could be moved from gestation pen to farrowing crate was measured using an arbitrary scale with objective definitions. It was thought that the ease of movement score might detect differences between sows in their maternal style.
7. Sows and gilts varied in size and so the amount of space available in the farrowing crate, relative to the sow or gilt, also varied between litters. In order to quantify this source of variation, the length of each sow and gilt was measured from video and adjusted to an estimated real-life length using the known crate dimensions.
8. The behaviour of sows and gilts was analysed from -24 hours pre-farrowing until 24 hours following the birth of the first piglet. Information relating to the frequency of the different types of posture changes, time spent in each activity, frequency of occurrence of behavioural events and the mean duration of each behavioural state was recorded from video.

CHAPTER 3:

PRE-FARROWING BEHAVIOUR OF SOWS

Introduction

Pre-farrowing behaviour in the sow is characterised by the preparations the sow makes to create a safe birthing area. The process starts with the selection of a nest-site (Jensen, 1986). The female becomes more active, investigating the environment further away from the group and finally selecting a site that offers some shelter but with an open view to aid vigilance (Grundlach, 1968; Signoret et al., 1975; Stolba and Wood-gush, 1989). Having selected a site the sow then starts to gather nest materials such as straw, grass and other vegetation, rooting them into a pile and hollowing out the centre to create a place to lie (Signoret *et al.*, 1975; Stolba and Wood-gush, 1989). Jensen (1993) identified two distinct types of nest-building behaviour using factor analysis - preparatory behaviour such as standing, nosing and rooting the floor, and nest material manipulation such as walking, carrying and arranging substrates. Jensen (1993) argues that only the former is influenced by internal cues, whereas the latter type of nesting behaviour requires external cues such as nest material. Although Jensen (1993) bases his argument on the lack of 'vacuum carrying and arranging' in barren environments, behaviours that are likely to be almost impossible to define, his argument is supported by the lack of gathering and carrying behaviours in the prostaglandin-induced nest-building model (Gilbert and Burne, 2000).

Nest-building behaviour is common to Wild Boar (Sambraus, 1978), feral pigs (Grundlach, 1968), extensively reared domestic pigs (Stolba, 1982) and intensively reared domestic pigs (Signoret *et al.*, 1975). Although the behaviour of intensively-reared pigs is frequently limited by the environment, the peri-parturient sow restrained in a farrowing crate will still attempt to utilise whatever materials are available to her to build a nest (Signoret *et al.*, 1975; Hartsock and Barczewski,

1997). The initial stages of nesting behaviour are influenced by the sows endocrine state (Jensen, 1993; Boulton *et al.*, 1997; Gilbert and Burne, 2000), therefore welfare problems are likely to arise from the restraint of this behaviour (The Brambell Report, 1965; Agricultural Committee, 1981). Higher levels of cortisol amongst sows attempting to nest-build in bare crates compared with larger straw pens supports this argument of physiological stress and indicates that the sows attempts to nest-build in crates without straw are not adequate substitutes for real nest-building (Lawrence et al., 1994; Boulton *et al.*, 1997).

Nest-building behaviour is one way a mother can invest into the survival of her offspring (Clutton-Brock, 1991). This investment carries with it costs to the mother. These are the energetic cost of selecting a nest site and building the nest and, in the wild, the increased risk of predation resulting from spending time away from the group and from collecting nest materials (a behaviour that competes with vigilance). In some domestic animals (rabbits), a well-formed nest has been shown to improve neonatal survival (Hamilton *et al.*, 1997). Maternal nest quality appears to be a trait influenced by genetics as breed studies in rabbits (Hamilton *et al.*, 1997) and studies on mice with specific gene deletions (or 'knock-outs') have shown (e.g. Lefebvre *et al.*, 1998). There is also some evidence that pig breeds might differ in their pre-farrowing behaviour. In farrowing crates, Meishan sows spend more time engaged in floor-directed behaviour 24 hours prior to farrowing than Large White sows (Meunier-Salaun *et al.*, 1991), although these differences were not found to hold for straw pens (Schouten and Meunier-Salaun, 1990).

The fact that parity one gilts, given no previous experience of nests or nest-building, will still try to build a nest on the day before farrowing (Signoret *et al.*, 1975), suggests that the nest-building has a genetic basis. Nests made by gilts tend to be less elaborate than those made by multiparous sows (Grauvogl, 1958), indicating that nest-building behaviour can be modified by experience. The presence of straw can also influence pre-farrowing behaviour of sows and gilts. Straw leads to less time spent standing, more time spent lateral lying (Cronin *et al.*, 1993), less floor-directed behaviour and less fixture-directed behaviour (Cronin and Van Amerongen, 1991;

Cronin *et al.*, 1993; Appleyard *et al.*, 1999; see also Lawrence *et al.*, 1994). Straw also leads to more total nesting behaviour (Cronin and Van Amerongen, 1991; Cronin *et al.*, 1993), although total nesting behaviour can be difficult to define. Cronin *et al.* (1993) used the definition "paw, root/nose" the crate or pen fixtures and floor plus the total "straw-directed behaviours". However, more recent research has failed to find an effect of straw on total nesting behaviour using very similar measures to Cronin (total straw, floor and fixture-directed behaviour) (Dr. S Jarvis, pers. comm.).

The current experiment was designed to explore the influence of straw, parity and breed on the expression of pre-farrowing nest-building behaviour. There is some evidence that the pre-farrowing cortisol response mentioned above is not as marked in the second parity compared to the first (Jarvis *et al.*, in press). This suggests that sows might be able to adapt their behaviour or their motivational goals to reduce the discrepancy between what the sow would like to achieve and what the sow can achieve, given the current restrictions. If adaptation to farrowing crate conditions does occur, and prior experience is important, then we might expect more evidence of adaptation from sows whose farrowing environment was identical over subsequent parities. Thus, the pre-farrowing behaviour of parity two sows with straw may depend on whether those sow experienced nest building in a crate with straw in her first parity. Similarly, the pre-farrowing behaviour of parity two sows without straw may depend on whether they experienced not have straw during parity one.

In the context of maternal quality we might expect good mothers to put more effort into the construction of a nest than poor mothers, especially if maternal quality has a genetic basis. In chapter 6 I will discuss the relationships between pre-farrowing behaviour and piglet mortality, an absolute measure of maternal quality. However, in this chapter, comparisons between pre-farrowing behaviour and maternal quality are made at the breed level. Breeds with high alleged maternal quality such as the Meishan and Meishan synthetic (Schouten and Meunier-Salaun, 1990; van der Steen and de Groot, 1992; Zou *et al.*, 1992; Sinclair *et al.*, 1996, 1998) are compared with

breeds not usually associated with good maternal quality such as the Duroc (Dr. A. D. Hall, Cotswold Pig Development Company, pers. comm.).

Experimental Design

The experiment was based around a breed by parity by treatment factorial design whereby individual sows were observed over two parities. The design was unbalanced largely as a result of sows 'dropping out' between parities (see Chapter 2). Treatment was the presence or absence of straw that was allocated randomly within breeds (see Chapter 2).

Behavioural Observations

The behaviour of 96 parity one and 63 parity two sows, farrowing between April 1998 and April 2000, was observed over eleven 10-minute periods from -24 hours until the onset of parturition. Fifty-seven of the parity two sows were also observed in parity one.

The sample of sows consisted of four breeds: Duroc pure (n = 55), Meishan pure (n = 17), Landrace-Duroc synthetic (n = 16) and Landrace-Meishan synthetic (n = 71). (See Chapter 2 for descriptions of these breeds.)

Statistical Analysis

The eleven 10-minute time samples were collapsed into four blocks in order to (a) average out extreme measurements, and (b) free up degrees of freedom so that more terms could be added to the statistical model.

The four blocks were:

1. -24, -20 hours (frequencies were multiplied by 1.5 to be equivalent to the other time blocks)
2. -16, -14, -12 hours
3. -10, -8, -6 hours
4. -4, -2, 0 hours

Restricted Maximum Likelihood (REML: Genstat, Version 5, Release 4.1, 1998, Lawes Agricultural Trust) tests were used to analyse the unbalanced factor groups, largely caused by not all parity one gilts being seen in parity two.

The REML analysis was a mixed model containing both fixed and random effects. The fixed effects specified were parity, breed, treatment and time sample plus the factors listed in Table 3.1. The random effects specified described the structure of the data set, i.e. sow nested within parity nested within time (sow/parity/time).

Fixed effect terms with non-significant Wald statistics (Chi-squared distribution) were removed from the model and the model was refitted to the data. The term of interest was always specified last in the model, thus controlling for all other influencing factors on a particular behaviour. The final models fitted are summarised in the appendix.

Table 3.1: Additional factors added to the statistical model. All of which could be measured but not controlled.

Factor	Description
Time of parturition	Time of day when the first piglet was born. 4 groups: 1. 0701 – 1300 (n = 33) 2. 1301 – 1900 (n = 63) 3. 1901 – 0100 (n = 35) 4. 0101 – 0700 (n = 28)
Season	Time of year of parturition. Four levels: 1. Dec - Feb (n = 32) 2. Mar - May (n = 60) 3. Jun - Aug (n = 28) 4. Sep - Nov (n = 39)
Age of sow	Age of sow at farrowing (min = 256 days, max = 856 days). Partially confounded with parity. Five levels: 1. 256 – 355 (n = 24) 2. 356 – 455 (n = 64) 3. 456 – 555 (n = 31) 4. 556 – 655 (n = 35) 5. ≥ 656 (n = 5)
Ease of movement score	Stockperson's score based on how difficult it was moving the sow from gestation pen to farrowing crate. Scored from 1 to 5 (see methods for definitions used). Sample sizes: 1. n = 33 2. n = 98 3. n = 23 4. n = 2 5. n = 2
Farrowing house	Which farrowing house the sow farrowed in. Old (n = 121) versus new (n = 38) (see chapter 2 for descriptions).
Radio	Whether or not a radio was playing in the farrowing house at the time the sow was nest building. Yes (n = 117), no (n = 42).
Days in the crate prior to BFP	Variation between the litters in the length of time the sow or gilt was in the crate prior to the onset of parturition. Six levels: 1. < 3 days / 72 hours (n = 37) 2. 3 - 4 days (n = 29) 3. 4 - 5 days (n = 22) 4. 5 - 6 days (n = 27) 5. 6 - 7 days (n = 15) 6. > 7 days (n = 28)

To investigate whether parity one treatment (straw versus no straw) had an effect on parity two behaviour, parity two data was analysed for differences between four treatment groups:

1. SS (n = 17) - sows given straw for both parities
2. SN (n = 13) - sows given straw in parity one and no straw in parity two
3. NS (n = 13) - sows given no straw in parity one and straw in parity two
4. NN (n = 14) - sows given no straw for both parities

This level of analysis could only be performed on two breeds, Meishan-Landrace and Duroc pure, due to the small sample size of the Landrace-Duroc breed and the absence of parity two data for the Meishan pure.

The structure of the data was tested for normality and homogeneity of variance using post-hoc normal plots, histograms of residuals and graphs of residuals and fitted values.

Results

The results are described in terms of the effects of the main experimental factors of breed, parity and treatment and their interactions with each other and the observational time sample. The terms included in the final REML model, describing each behaviour variable, are summarised in the appendix. Most of the factors listed in Table 3.1 had little or no influence on the sample variance and so were dropped from the final model.

Breed Effects

The breed differences found in the pre-farrowing behaviour of sows and gilts in this study are summarised in Table 3.2. These breed differences were consistent over all time periods within parity but only time spent inactive and the two measures of fixture-directed behaviour showed consistency within individuals over two parities. There were no breed by treatment interactions.

Table 3.2: Breed differences in pre-farrowing behaviour. Breeds represented are pure Duroc (D), Landrace-Duroc (LD), Meishan-Landrace (ML) and pure Meishan (M). Breed means are back-transformed REML estimates (with 95% confidence intervals) controlled for repeated measures, parity, time period, treatment, time of farrowing and age of sow. Means with different suffixes are statistically different at $p<0.05$. The sow variance component, when significantly greater than 0, indicates individual consistency over parities.

Behaviour (per 30 minutes)	**Sow variance component ($x\ 10^{-3}$)**	**Breed Means (95% confidence intervals)**			
		D (n = 55)	**LD (n = 16)**	**ML (n = 71)**	**M (n = 17)**
% inactive	8.0 +/- 4.3	$44.9\%^{a}$ (42.5 – 47.3%)	$41.9\%^{ab}$ (37.8 – 46.1%)	$34.7\%^{b}$ (32.6 – 36.8%)	$40.5\%^{ab}$ (36.4 – 44.7%)
% head-move	2.2 +/- 2.9	$34.4\%^{a}$ (32.6 – 36.1%)	$36.6\%^{ab}$ (33.5 – 39.7%)	$45.4\%^{b}$ (43.7 – 47.0%)	$39.5\%^{ab}$ (36.4 – 42.7%)
% sit	0.3 +/- 1.6	$3.18\%^{a}$ (2.71 – 3.69%)	$5.05\%^{ac}$ (4.04 – 6.16%)	$8.55\%^{b}$ (7.87 – 9.27%)	$7.11\%^{bc}$ (5.92 – 8.41%)
% fixture-directed	1.4 +/- 0.8	$2.01\%^{ac}$ (1.74 – 2.30%)	$1.39\%^{c}$ (1.01 – 1.83%)	$2.82\%^{ab}$ (2.53 – 3.13%)	$3.83\%^{b}$ (3.19 – 4.53%)
Freq. fixture-directed	15.4 +/- 7.0	2.90^{ac} (2.70 – 3.12)	1.96^{c} (1.73 – 2.22)	3.58^{ab} (3.35 – 3.82)	4.79^{b} (4.23 – 5.42)

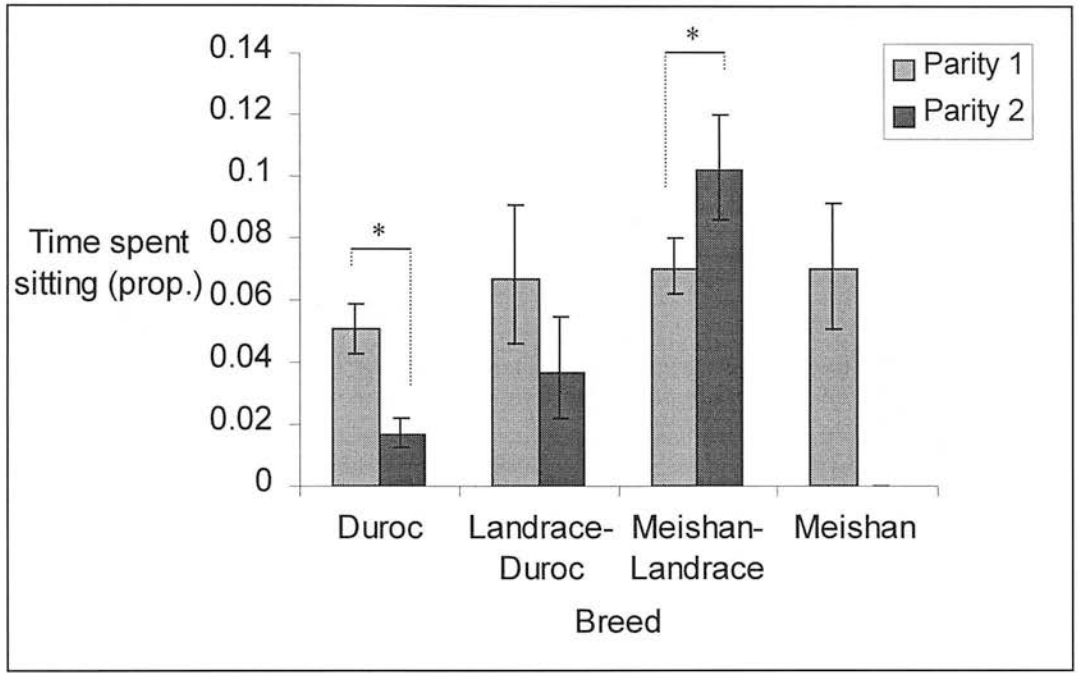
Meishan-Landrace sows spent less time inactive ($t_{124} = 2.84$, $p<0.01$) during the 24 hours pre-farrowing period than Duroc sows, and this difference in activity was due to a behavioural state known as 'head-move' ($t_{124} = 4.06$, $p<0.001$) (see the ethogram in Chapter 2 for a definition of this behaviour and Table 3.2 for values).

Both the Meishan-Landrace breed ($t_{124} = 5.68$, $p<0.001$) and the Meishan pure ($t_{70} = 3.01$, $p<0.01$) spent more time sitting than the Duroc breed, whilst the Meishan-Landrace breed also spent more time sitting than the Landrace-Duroc cross ($t_{85} = 2.40$, $p<0.02$) (see Table 3.2 for values).

The Meishan pure spent more time mouthing the crates' bars and fixtures and at a higher frequency than both the Duroc (t_{70} = 2.57, $p<0.02$) and Landrace-Duroc composite breed (t_{31} = 3.20, $p<0.01$) over all time periods. Meishan-Landrace sows spent more time mouthing the crate bars and fixtures than Landrace-Duroc sows (t_{75} = 2.38, $p<0.05$) (see Table 3.2 for values). These breed differences were also mirrored in the frequencies with which the sows began a period of fixture-directed behaviour (see Table 3.2 for values).

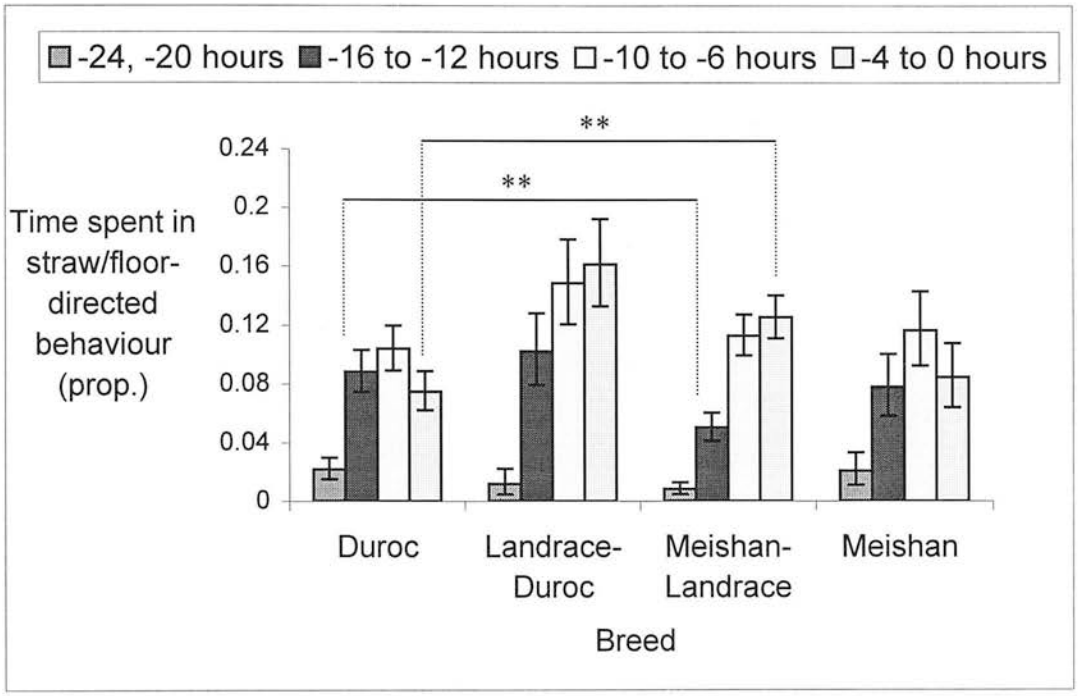
In addition to these main breed effects displayed in Table 3.2, there was a significant breed-parity interaction for time spent sitting (W_2 = 15.0, $p<0.001$). Durocs spent less time sitting in parity two than in parity one (t_{54} = 2.43, $p<0.02$), Landrace-Duroc sows spent similar amounts of time sitting during the two parities, and Meishan-Landrace sows spent more time sitting in parity two than in parity one (t_{69} = 2.17, $p<0.05$) (see Figure 3.1).

Figure 3.1: Breed by parity interaction for time spent sitting during the 24 hour pre-farrowing period. Values are back-transformed REML estimates (+/- 95% confidence intervals) controlled for season, treatment, age of sow, farrowing house and all other factors listed in Table 3.1. * = $p<0.05$



Within certain time periods, there were also breed differences in straw- and floor-directed behaviour. During the second time block, -16 to -12 hours, Duroc sows performed more straw and floor-directed behaviour than Meishan-Landrace sows (t_{124} = 2.7, $p<0.01$) (see Figure 3.2). Whilst during the fourth time block, -4 to 0 hours, Duroc sows performed less straw and floor-directed behaviour than both Meishan-Landrace sows (t_{124} = 2.7, $p<0.01$) and Landrace-Duroc sows (t_{69} = 2.6, $p<0.05$) (see Figure 3.2). These differences resulted in a small but significant breed-time interaction (W_9 = 17.3, $p<0.05$). Differences between Meishan-Landrace and Duroc sows in time spent interacting with straw and floor were also mirrored in the frequency of straw and floor-directed behaviour.

Figure 3.2: Breed by time period interaction on the time spent interacting with the straw or floor of the farrowing crate. Values are back-transformed REML estimates controlled for repeated measures, parity, treatment, season, time of day, farrowing house, age of sow and all other factors listed in Table 3.1. ** = $p<0.01$



Breed differences also existed within time period for frequency of stepping – a measure of the locomotor part of nest building. During the first time period, -24 and –20 hours, Meishan sows stepped more (5.2, 95% Confidence Interval = 4.0 - 6.9) than Duroc sows (2.6, 95% CI = 2.2 - 3.1; $t_{70} = 2.1$, $p<0.05$). In the last time period, -4 to 0 hours, Meishan-Landrace sows stepped more (12.9, 95% CI = 11.2 - 14.8) than Duroc sows (5.8, 95% CI = 4.9 - 6.8; $t_{124} = 3.9$, $p<0.001$). Overall there was a small but significant breed-time interaction ($W_9 = 17.2$, $p<0.05$).

Parity Effects

Many parity effects were dependent on time period, so Table 3.3 summarises these effects by displaying parity means within time period. There behavioural activity appeared to be more focussed towards the later time periods in parity 2 compared to parity 1.

Table 3.3: Parity effects and parity-time interactions on four pre-farrowing behaviour measures. The percentage time spent during each time block is presented (+/- 95% confidence intervals). Values are back-transformed REML estimates controlled for repeated measures, breed, treatment and all factors listed in Table 3.1. P-values for parity effects within time block, are based on the t-distribution. P-values for the parity by time interaction term are based on the Chi-squared distribution on 3 degrees of freedom.

Behaviour	**Parity effect**	**Time Block**				**Parity by time p-value**
		-24, -20	**-16, -14, -12**	**-10, -8, -6**	**-4, -2, 0**	
Inactive	**P 1**	58.0% (54.8-61.1%)	33.8% (30.8-36.8%)	22.5% (19.9-25.2%)	30.9% (28.0-33.8%)	<0.01
	P 2	76.5% (73.8-79.2%)	53.5% (50.4-56.7%)	32.6% (29.7-35.6%)	30.7% (27.8-33.6%)	
	p-value	**<0.001**	**<0.001**	**<0.02**	**>0.05**	
Kneel	**P 1**	0.75% (0.63-0.89%)	1.03% (0.89-1.19%)	0.71% (0.59-0.84%)	0.67% (0.56-0.80%)	<0.001
	P 2	0.03% (0.01-0.07%)	0.48% (0.39-0.59%)	0.74% (0.62-0.87%)	1.01% (0.87-1.16%)	
	p-value	**<0.001**	**<0.001**	**>0.05**	**>0.05**	
Lateral lie	**P 1**	42.2% (37.9-46.5%)	20.3% (16.9-23.9%)	23.8% (20.1-27.6%)	40.4% (36.2-44.8%)	<0.01
	P 2	61.3% (57.0-65.5%)	30.1% (26.1-34.1%)	21.2% (17.8-24.9%)	38.8% (34.5-43.1%)	
	p-value	**<0.01**	**>0.05**	**>0.05**	**>0.05**	
Sit	**P 1**	4.35% (2.97-5.97%)	9.90% (7.81-12.20%)	6.61% (4.90-8.55%)	8.18% (6.28-10.30%)	<0.05
	P 2	0.49% (0.11-1.14%)	2.86% (1.76-4.21%)	3.95% (2.64-5.50%)	4.76% (3.32-6.45%)	
	p-value	**<0.01**	**<0.01**	**>0.05**	**>0.05**	

Parity by time period interactions were also found for time spent inactive ($W_3 = 17.1$, $p<0.001$), kneeling ($W_3 = 42.0$, $p<0.001$), sitting ($W_3 = 12.3$, $p<0.01$) and lying laterally ($W_3 = 11.4$, $p<0.01$) (see Table 3.3).

During -24 and -20 hour samples, parity two sows spend less time kneeling ($t_{157} = 6.52$, $p<0.001$), less time sitting ($t_{157} = 2.69$, $p<0.01$) and more time inactive ($t_{157} = 4.45$, $p<0.001$) and lying laterally ($t_{157} = 3.11$, $p<0.01$) than parity one gilts. Between -16 and -12 hours, parity 2 sows spent more time inactive ($t_{157} = 4.47$, $p<0.001$), less time sitting ($t_{157} = 2.88$, $p<0.01$) and less time kneeling ($t_{157} = 3.07$, $p<0.01$) than parity 1 gilts. Between -10 and -6 hours, parity 2 sows still spent slightly more time inactive than parity 1 gilts ($t_{157} = 2.53$, $p<0.02$) but there was no difference at this stage in time spent sitting, kneeling or lying laterally between parities. Between -4 and the onset of parturition (0 hours), parity two sows spent similar amounts of time inactive, sitting, lateral lying and kneeling as parity one gilts (see Table 3.3. for means and 95% confidence intervals).

Parity by time period interactions were also found for time spent standing ($W_4 = 46.6$, $p<0.001$) and frequency of stepping ($W_4 = 29.8$, $p<0.001$) (see Figures 3.3 and 3.4). Between -24 and -12 hours, parity two sows spent less time standing (-24 to -20, $t_{157} = 4.3$, $p<0.001$; -16 to -12, $t_{157} = 2.6$, $p<0.01$) and stepped less frequently (-24 to -20, $t_{157} = 3.1$, $p<0.01$; -16 to -12, $t_{157} = 2.7$, $p<0.01$) than parity 1 gilts. Whereas between -10 hours and the onset of parturition, there were no significant parity differences for time spent standing and frequency of stepping (see figures 3.3 and 3.4 for values and 95% confidence intervals).

Straw and floor-directed behaviour ($W_3 = 12.5$, $p<0.01$) and fixture-directed behaviour ($W_3 = 30.5$, $p<0.001$) also had parity by time period interactions (see Figures 3.5 and 3.6). During the first two time periods, -24 to -12 hours, parity two sows spent less time interacting with the straw or floor than parity one gilts (-24 to -20 hours, $t_{157} = 2.2$, $p<0.05$; -16 to -12 hours, $t_{157} = 2.8$, $p<0.01$) (see Figure 3.5). During the same time period, parity two sows spent less time mouthing and nosing the crate bars and fixtures than parity one gilts (-24 to -20 hours, $t_{157} = 2.10$, $p<0.05$;

-16 to -12 hours, t_{157} = 5.62, p<0.001) (see Figure 3.6). From -10 hours until the onset of parturition there was no difference between the parities in time spent engaged in straw and floor-directed behaviour. Similarly, between -10 and -6 hours there was no difference between the parities in time spent mouthing and nosing the crates bars and fixtures. However, during -4 and 0 hours pre-farrowing, parity two sows spent more time mouthing and nosing the crates bars and fixtures than parity one gilts (t_{157} = 3.37, p<0.001) (see Figure 3.6 for values and 95% confidence intervals).

Figure 3.3: Mean time spent standing (+/- 95% confidence intervals) over the four pre-farrowing time blocks and for parity one and parity two sows. Values are back-transformed REML estimates, controlled for repeated measures, breed, treatment and all factors listed in Table 3.1. There was a significant parity by time interaction (W_4 = 46.6, p<0.001). Between parity comparisons: ** = p<0.01, *** = p<0.001.

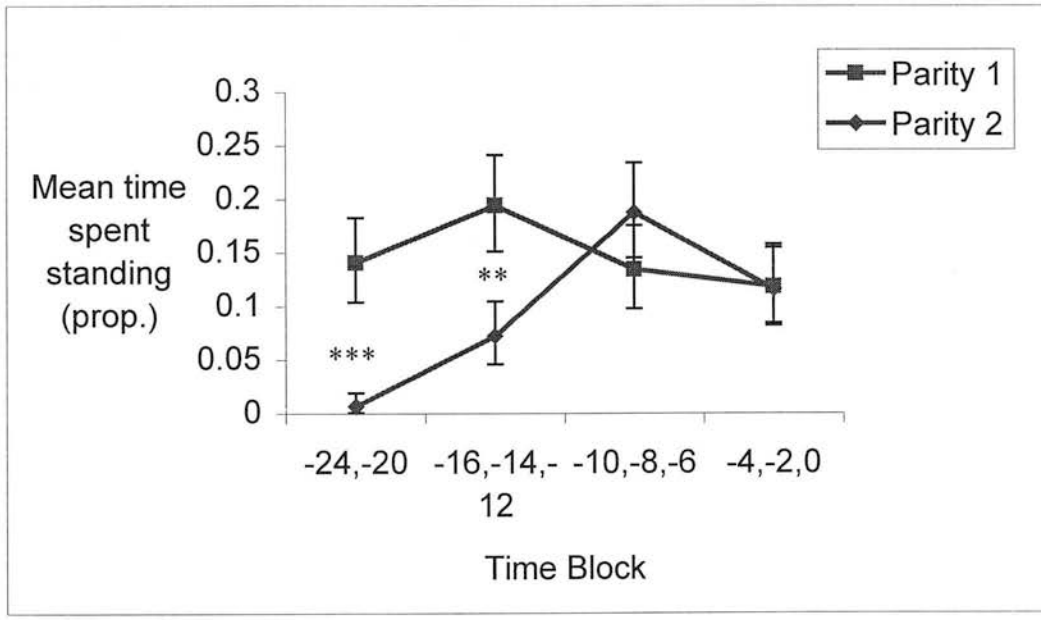


Figure 3.4: Mean frequency of stepping (+/- 95% confidence intervals) over the four pre-farrowing time blocks and for both parity one and parity two sows. Values are back-transformed REML estimates, controlled for repeated measures, breed, treatment and all factors listed in Table 3.1. There was a significant parity by time interaction (W_4 = 29.8, $p<0.001$). Between parity comparisons: ** = $p<0.01$

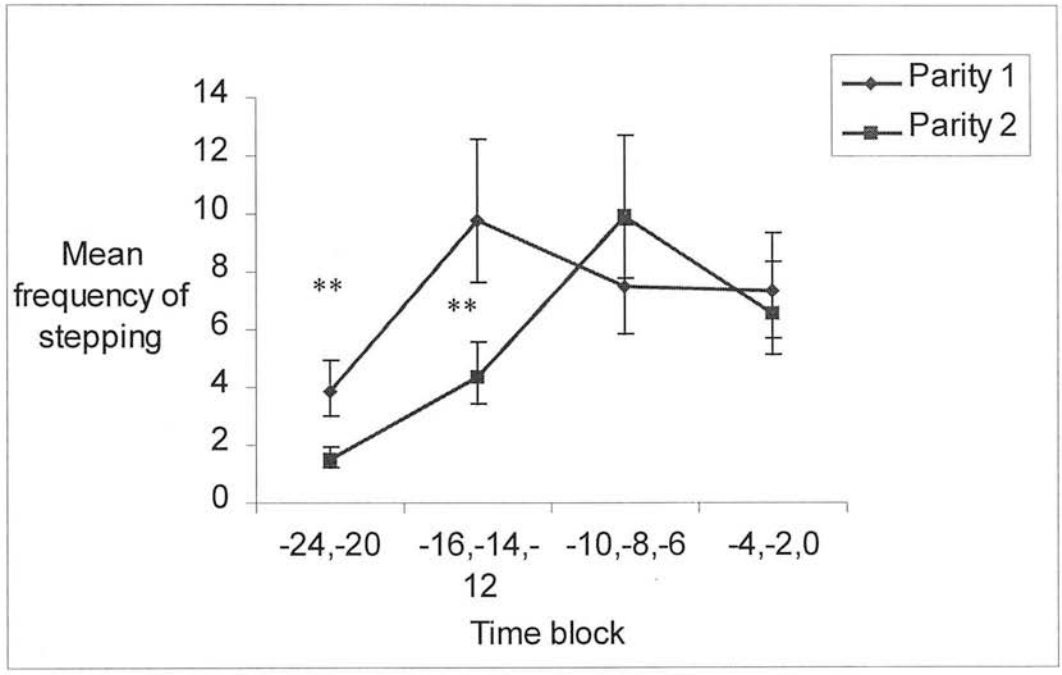


Figure 3.5: Mean time spent in straw- and floor-directed behaviour over 4 time blocks and for parity one gilts and parity two sows. Values back-transformed REML estimates (+/- 95% confidence intervals), controlled for repeated measures, breed, treatment and all factors listed in Table 3.1. There was a significant parity-time interaction ($W_3 = 12.5$, $p<0.01$).
Between parity comparisons: * = $p<0.05$, ** = $p<0.01$

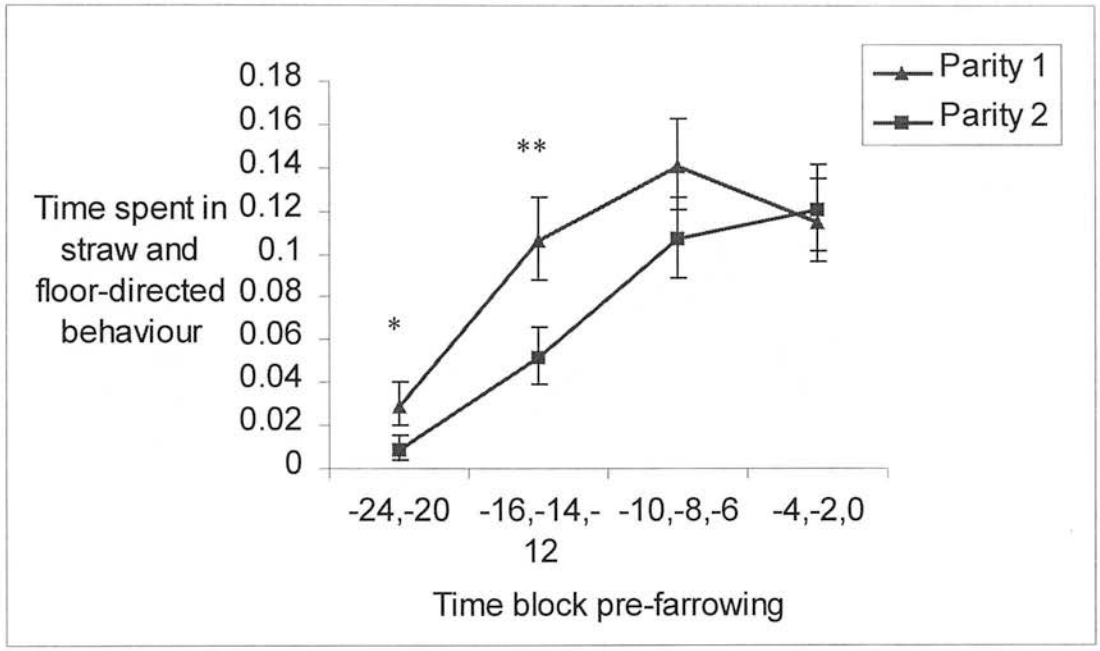
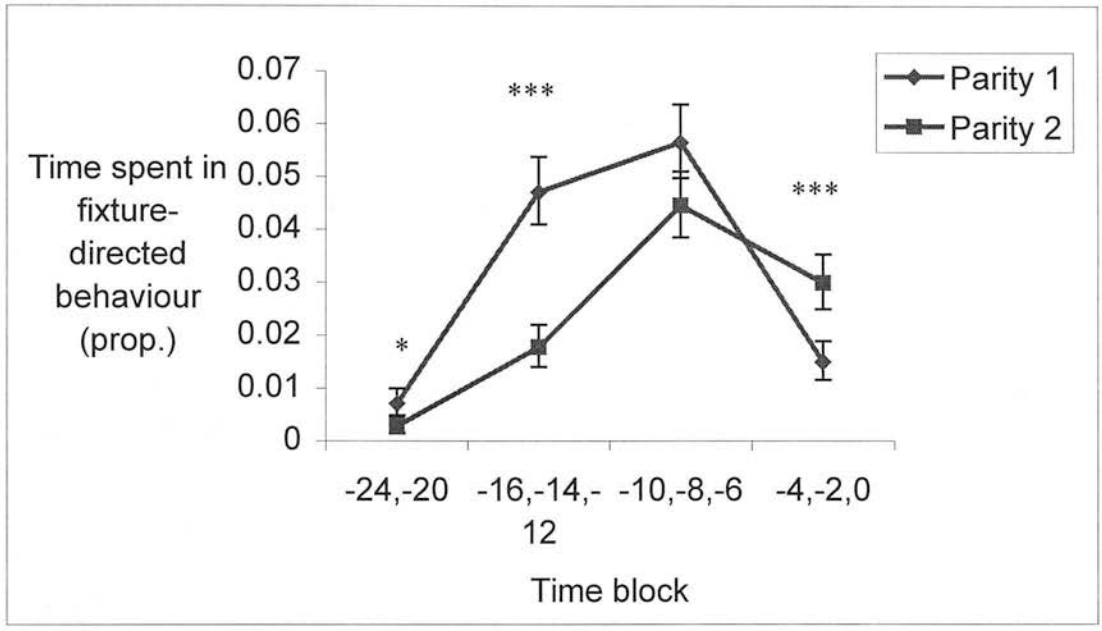


Figure 3.6: Mean time spent interacting with the crate bars and fixtures over four time blocks during the pre-farrowing period in both parity one and parity two sows. Values are back-transformed REML estimates (+/- 95% confidence intervals), controlled for repeated measures, breed, treatment and all factors listed in Table 3.1. There was a significant parity-time interaction (W_3 = 30.5, $p<0.001$). Between parity comparisons: * = $p<0.05$, *** = $p<0.001$



Straw Effects

All treatment (straw versus no straw) effects were found in the substrate-directed behaviours only. The presence of straw had no effect on the time spent in any one of the postures identified or levels of general activity. Table 3.4 summarises the straw effects found after controlling for breed, parity and time period effects. There was only one treatment by time interaction, this was a weak interaction on the frequency of fixture-directed behaviour (W_3 = 8.4, $p<0.05$). During -4 to 0 hours only, sows without straw started periods of fixture-directed behaviour more frequently (4.0, 95% CI = 3.6 - 4.4) than sows with straw (2.9, 95% CI = 2.6 - 3.2; t_{157} = 2.2, $p<0.05$).

Table 3.4: Effects of straw in the farrowing crate on the pre-farrowing substrate-directed behaviours. Back-transformed REML estimates are presented (with 95% confidence interval), controlled for repeated measures, parity, breed, time period and all factors in Table 3.1.

Behavioural measure	**Treatment p-value (χ^2)**	**Treatment Means (95% confidence intervals)**	
		Straw	**No Straw**
Proportion of **total substrate**-directed behaviour	<0.02	12.5% (11.5 - 13.7%)	8.9% (8.0 - 9.9%)
Proportion of **fixture**-directed behaviour	<0.05	2.80% (2.43 - 3.19%)	3.97% (3.53 - 4.43%)
Proportion of **straw/floor**-directed behaviour	<0.001	9.55% (8.70 - 10.44%)	4.96% (4.34 - 5.63%)
Frequency of **fixture**-directed behaviour	>0.05	3.1 (2.8 - 3.3)	3.4 (3.2 - 3.7)
Frequency of **straw/floor**-directed behaviour	<0.001	4.6 (4.3 - 4.9)	3.2 (3.0 - 3.5)
Bout length, **fixture**-directed behaviour	<0.05	7.3 seconds (6.3 - 8.5 s)	10.9 seconds (9.6 - 12.4 s)
Bout length, **straw/floor**-directed behaviour	<0.01	31.4 seconds (28.6 - 34.4 s)	19.5 seconds (17.2 - 21.8 s)

The presence of straw was associated with more time spent in straw and floor-directed behaviour, along with a greater frequency of occurrence and longer means bout length of straw and floor-directed behaviour. The absence of straw was associated with more time spent in fixture-directed behaviour, along with a greater frequency of occurrence of and longer means bout length of fixture-directed behaviour.

Combining straw, floor and fixture behaviours gives us total substrate-directed behaviour. Sows given straw spent slightly more time performing substrate-directed behaviour than sows without straw. Since there was no treatment by time interaction for this measure, sows with straw must have spent more time in total substrate-directed behaviour over all time periods.

In order to investigate whether sows that showed attempted **escape behaviour** (climbing the crate bars and trough or sliding underneath the crate bars) performed more substrate-directed behaviour, **escape** was included in the REML analysis as a binary level factor. Escape attempts were seen in 41 of the 159 farrowings analysed. Sows that performed at least one escape behaviour performed significantly more fixture-directed behaviour (4.8%, 95% CI = 4.0 - 5.7%) than sows that were never seen making an attempted escape (2.1%, 95% CI = 1.9 - 2.4; $t_{157} = 4.03$, $p<0.001$). There was no difference between sows that showed escape attempts and those that did not in the amount of straw or floor-directed behaviour seen.

Experience of nest building in crates without straw during parity one influenced the expression of fixture-directed behaviour in crates without straw during the pre-farrowing period of parity two. This effect was breed-dependent, present in Duroc but not Meishan-Landrace, and time-dependent, occurring only during the -10 to -6 hour time block (see Figures 3.7 and 3.8 for details). During this time period, Duroc parity two sows without straw, which had previously farrowed in a crate without straw, spent more time in fixture-directed behaviour ($t_8 = 3.31$, $p<0.02$) than if they had experienced straw in parity one (see Figure 3.7 for values and 95% confidence intervals).

During this time period, Duroc parity two sows in crates without straw would spend more time inactive if they had experienced straw (71.8%, 95% CI = 63.0 - 79.8%) during the pre-farrowing period of parity one than if they had not experienced straw (14.8%, 95% CI = 8.8 - 22.1%; $t_8 = 2.46$, $p<0.05$). A similar effect was not seen for Meishan-Landrace parity two sows.

This breed-dependent effect parity effect is summarised in the following diagram:

Duroc Sows, -10 to -6 hours pre-farrowing:

Parity 1:	No straw	Straw
	⇓	⇓
Parity 2:	No straw	No Straw
Behaviour change	*More fixture-directed in p2*	*More inactive in p2*

There were no residual effects of experience of straw in parity one on the behaviour of parity two sows.

Figure 3.7: The expression of fixture-directed behaviour amongst parity two Duroc sows with no straw in the farrowing crate. This behaviour appears to be influenced by whether or not the sow experienced straw (n = 5) or not (n = 5) during the pre-farrowing period of parity one. Values back-transformed REML estimates (+/- 95% confidence intervals), controlled for repeated measures and all factors listed in Table 3.1. * = $p<0.01$

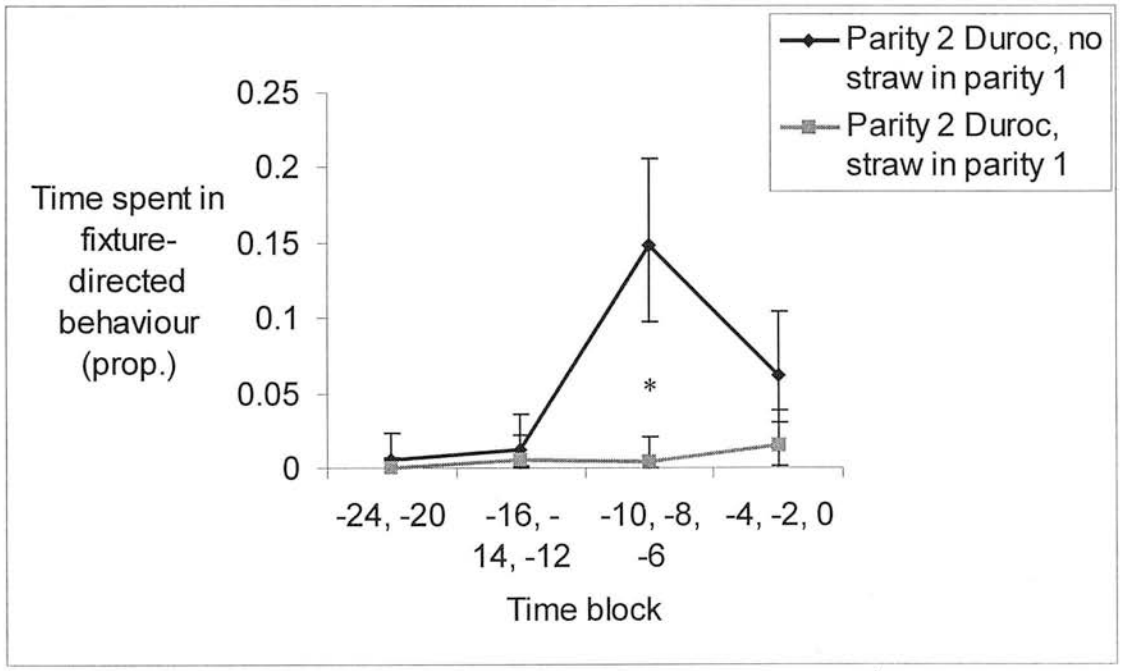
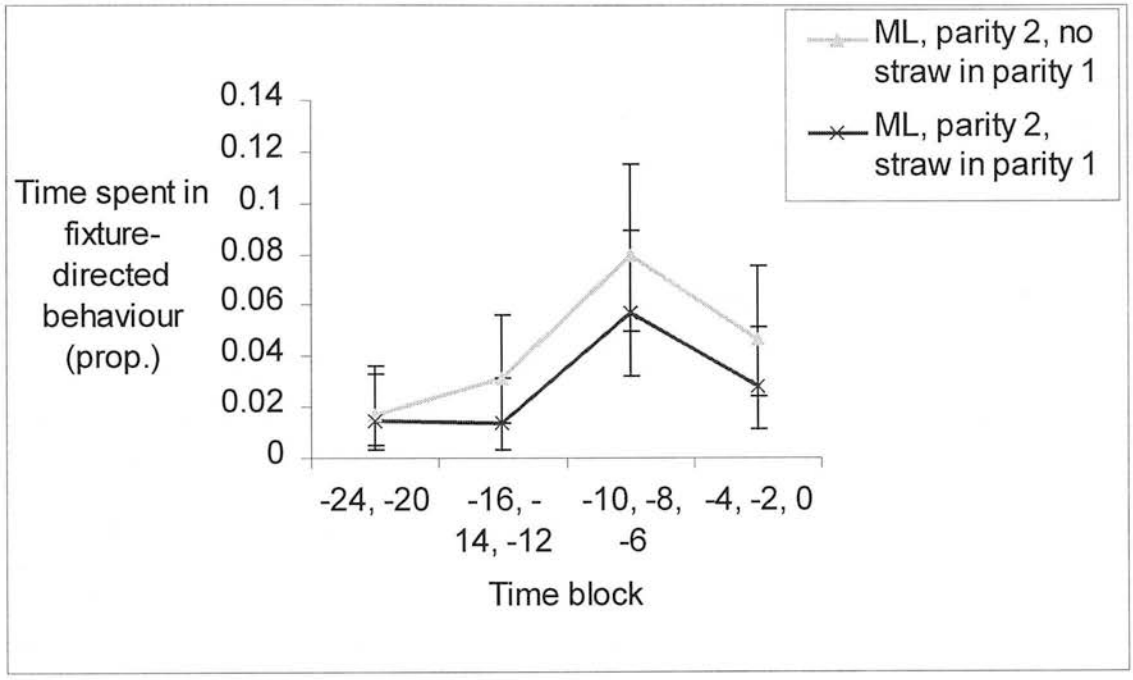


Figure 3.8: The expression of fixture-directed behaviour amongst parity two Meishan-Landrace (ML) sows with no straw in the farrowing crate. Sows are grouped as to whether they had straw (n = 11) or not (n = 8) during the pre-farrowing period of parity one. Values are back-transformed REML estimates (+/- 95% confidence intervals), controlled for repeated measures and all factors listed in Table 3.1.



Discussion

Nest building behaviour is indicated by the performance of the substrate-directed behaviours (straw, floor and fixtures), the standing posture and stepping (Jensen, 1993; Cronin *et al.*, 1994; Boulton *et al.*, 1997; Hartsock and Barczewski, 1997). The total performance of most of these behaviours over 24 hours did not vary between breeds, indicating that all breeds invest a similar amount of effort into this maternal behaviour. The expression of fixture-directed behaviour was an exception but this may be because fixture-directed behaviour is not solely governed by nest building motivation.

The presence of straw allowed the sow to engage in more activities, such as carrying, eating and pushing straw around, which resulted in more straw and floor-directed behaviour. This increase in the expression of straw and floor-directed behaviour was made at the expense of performing less fixture-directed behaviour, suggesting that some fixture-directed behaviour is motivated by nest building motivation. This effect of straw has been reported extensively in the literature (Cronin and Van Amerongen, 1991; Cronin *et al.*, 1993; Jensen, 1993; Appleyard *et al.*, 1999). Straw did not effect time spent standing or frequency of stepping, the other behavioural indicators of nest building. However, the presence of straw did result in more time spent in total substrate-directed behaviour (straw, floor and fixture-directed), indicating that nest-building behaviour is subject to environmental feedback. This result is in accordance with the majority of the background literature relating to the influence of straw on nest-building behaviour (Cronin and Van Amerongen, 1991; Arey, 1992; Jensen, 1993; Cronin *et al.*, 1993; Burne *et al.*, 2000).

Fixture-directed behaviour showed strong breed differences that were independent of time relative to parturition. In contrast, breed differences in the expression of straw and floor-directed behaviour, standing and stepping only emerged during certain times, resulting in breed by time interactions. Since fixture-directed behaviour did not follow the same breed by time interaction pattern as straw and floor-directed behaviour, standing and stepping, the underlying motivations of these behaviours

may be different. Fixture-directed behaviour was expressed more by sows and gilts that climbed or attempted to slide underneath the bars than sows and gilts that did not display these behaviours. Climbing the crate bars or attempting to slide underneath the crate bars are behaviours resulting in the sow's head reaching outside of the confines of the crate and so might be viewed as escape attempts. Therefore, sows and gilts that overtly show escape attempts perform more fixture-directed behaviour. In this study, Meishan and Meishan-Landrace sows spent more time engaged in fixture-directed behaviour than the Duroc and Landrace-Duroc breeds. Thus, genotype influences the expression of re-directed nest building or the overt expression of escape motivation.

The breed by time interactions for straw and floor-directed behaviour, standing and stepping show differences between the breeds in how they partition their nesting behaviour over time. In comparison with the Meishan-Landrace, Duroc sows begin their nest-building behaviour earlier relative to the start of parturition. These different patterns of nest building in the different breeds may arise out of differences in the hormonal profile of different breeds in relation to the hormones that promote nest building. Alternatively, it is possible that the farrowing crate inhibits the initiation of nest building behaviour in different breeds to different extents. Chapter 6 will examine the effect of pre-farrowing differences in the partitioning of nest building behaviour over time on the incidence of piglet mortality.

Breed differences over the entire 24 hour period were found in several behaviour measures, most strongly for measures of general activity and for time spent in the sit posture. Time spent sitting is heritable in pigs (McGlone *et al.*, 1991), so it is not surprising that we find breed differences here. Spending a lot of time in the sit posture has been previously associated with space-restrictive environments (Hansen and Curtis, 1981; Pearce and Paterson, 1993; Lembeck *et al.*, 1996). Passive sitting in pigs has also been associated with chronic intermittent electric shocks (Jensen *et al.*, 1996), frustration of feeding (Lewis, 1999) and physiological stress reactions (Dybkjaer, 1992). These results suggest that the welfare of sows and gilts that sit for long periods of time might be compromised. In this study the Meishan-Landrace and

the Meishan pure sat for longer periods of time than the Duroc pure. When standing up from a lying posture, pigs will usually enter a transitional sit posture but will move quickly on to a stand posture. Sows in farrowing crates tend to perform more lie-sit-lie sequences than sows in pens, which are more likely to continue to a standing position (Edwards *et al.*, 1986; Prof. S. A. Edwards, pers. comm.). Thus, sows in farrowing crates are more likely to truncate the process of standing up, which may be because once the sow is in a sitting position it becomes clear to her that gathering materials for a nest will not be possible. This is reminiscent of early ethological work on conflict behaviours (e.g. Tinbergen, 1952), where seemingly inappropriate behaviours (e.g. grooming) are expressed at times when two conflicting motivations (e.g. fight or flight) are at balance (Manning and Dawkins, 1992, p.82). The pre-farrowing sow's conflict is whether to nest-build in the confines of the crate (adapt her behaviour to suit the environment) or attempt to escape the crate in order to find a more suitable nesting site. Animals in such a position of conflict would be expected to have higher levels of cortisol (Dybkjaer, 1992; Lewis, 1999). The Meishan breed is known to have a more sensitive hypothalamo-pituitary-adrenal (HPA) axis than the Large White breed (Desautes et al., 1997, 1999), which is consistent with sows and gilts with Meishan genes sitting more.

Time spent sitting was also subject to a breed by parity interaction. Meishan-Landrace sows spend more time sitting in parity two than parity one, whilst Duroc sows spent less time sitting in parity two than parity one. This may indicate that Duroc sows adapt their nest building behaviour to the crate, through experience of the crate, in order to reduce motivational conflict. In contrast, Meishan-Landrace sows fail to adapt and show more signs of motivational conflict in parity two.

This study uncovered an effect of consistency of environment on the expression of fixture-directed behaviour that was both breed and time dependent. Duroc parity two sows farrowing in crates without straw and with prior experience of nest building in the absence of straw perform more fixture-directed behaviour than Duroc parity two sows with no such experience. This difference was found between -10 and -6 hours, considered to be around the time of maximal nest-building activity for most sows

(Thodberg *et al.*, 1999; Damm *et al.*, 2000). Therefore, the extra fixture-directed behaviour performed as a result of prior experience is likely to be re-directed nest building behaviour. A similar effect was not found for Meishan-Landrace sows as these animals expressed similar amounts of fixture-directed behaviour, over all pre-farrowing time periods, regardless of prior experience of nest-building without straw. This provides further evidence that Duroc sows can better adapt their nesting behaviour to the farrowing crate than Meishan-Landrace sows.

Interestingly, a similar effect resulting from experience of straw during in parity one and the expression of straw and floor-directed behaviour in parity two was not found. Therefore, unlike fixture-directed behaviour, the use of straw when motivated to nest-build does not seem to require a period of adaptation. This is likely to be because straw can be more readily identified as a potential nesting material (Damm *et al.*, 2000) than the bars of the farrowing crate.

Nest building in parity two appeared to be more focussed over a shorter time than nest building in parity one, suggesting that efficiency at nest-building comes with experience of nest-building. Parity two sows invest less time and energy in nest building, which may be because the sow has learnt that many components of nest building can not be performed in the crate. It would therefore be more adaptive to conserve energy for milk production and parturition.

Summary and Conclusions

1. The presence of straw is associated with more time being spent in total substrate-directed behaviour, behaviour thought to represent nest-building behaviour. This result is consistent with what other authors have found.
2. There were no breed differences in the total time spent performing most of the behavioural indicators of nest building over the whole 24-hour pre-farrowing period. Straw and floor-directed behaviour, standing and stepping were subject to breed by time interactions. Therefore, the partitioning of nest building behaviour in the crate over 24 hours pre-farrowing is subject to genotype differences.
3. Sows in crates with straw do more straw and floor-directed behaviour at the expense of doing less fixture-directed behaviour, indicating that some fixture-directed behaviour is governed by nest-building motivation
4. Fixture-directed behaviour exhibits breed differences that are not dependent on time relative to parturition, unlike the other behaviour indicators of nesting, indicating that not all fixture-directed behaviour is governed by nest-building motivation. There was a positive relationship between the expression of fixture-directed behaviour and the occurrence of behavioural escape attempts, indicating that escape motivation may underlie some fixture-directed behaviour.
5. Experience of farrowing in crates is associated with a focussing of nest-building behaviour, which may be more efficient and adaptive.
6. Prior experience of nest building in a crate without straw results in more fixture-directed behaviour for Duroc but not Meishan-Landrace sows, in parity two. This indicates genetic differences in a sows ability to adapt her nest building behaviour to the farrowing crate environment. This effect of prior experience resulted in more fixture-directed behaviour only during the time of maximum nest building activity, indicating that learnt response is to re-direct nesting motivation to the crate bars.
7. Breed differences exist for time spent sitting, a behaviour that would seem to reflect motivational conflict in the pig. Meishan and Meishan-Landrace sows spend more time sitting than Duroc and Landrace-Duroc sows. In addition, in the second parity Meishan-Landrace sows spend more time sitting and Duroc sows

spend less time sitting than in parity one. This suggests that the Duroc sow is better able to adapt her nesting behaviour to the farrowing crate than the Meishan-Landrace sow.

CHAPTER 4:

PARTURITION AND POST-FARROWING BEHAVIOUR

Introduction

The onset of parturition in the pig is associated with major behavioural and physiological changes. The physiological changes include a change of the position of opioid inhibition of oxytocin secretion from auto-inhibition at the neural lobe of the pituitary to inhibition at the level of the hypothalamus (see Lawrence *et al.*, 1997 for a review). Some of these physiological changes will be discussed in later Chapters. Behaviourally, the sow or gilt becomes less active and spends increasing amounts of time lying laterally as parturition approaches and through out the expulsive phase (Grundlach, 1968; Wood-Gush *et al.*, 1986; Fraser and Phillips, 1989; Rudd and Marchant, 1995).

Once piglets start to arrive, the reaction of sows, and especially gilts, to their piglets becomes an important consideration. Compared to other farm animals mother-offspring bonding is thought to be of limited importance in pigs since, being a nesting animal, piglets do not need follow the mother soon after birth (Lent, 1974; Signoret *et al.*, 1975). In natural conditions, sows and their piglets tend to leave the nest after about ten days (Jensen, 1988), by which time mother and offspring must be able to recognise each other. Sow-piglet bonding is thought to be established through suckling and nose contacts (Grundlach, 1968; Whatson and Bertram, 1983; Jensen and Redbo, 1987). In semi-natural conditions, it has been reported that mother-offspring bonds are developed by day six of age but piglets can recognise their mother within three to four days (Stangel and Jensen, 1991). However, there is evidence that recognition of a litter happens much earlier than this. For example,

cross-fostering is thought to be only successful, at reducing piglet mortality, if it happens soon after parturition (Graves, 1984; Straw *et al.*, 1998).

Litters of piglets are born with a wide range of birth weights (Fahmy and Bernard, 1971; English and Smith, 1975; Thompson and Fraser, 1988) and different degrees of viability (English and Wilkinson, 1982). These differences between piglets leads to some piglets have a competitive advantage over others for access productive teats (Fraser *et al.* 1995). The viability of a piglet, and risk of intra-partum death, is thought to be strongly influenced by the length of time it spent in the birth canal, with its oxygen supply restricted (English *et al.*, 1982). In addition, the viability of piglets, as measured by blood lactate levels, born later in the birth order appears to be lower than that of piglets born earlier in the birth order (English and Wilkinson, 1982). Therefore, variability in the length of birth intervals and long parturitions might lead to a bigger competitive asymmetry between litter mates. It has been suggested that this competitive asymmetry is an adaptive mechanism that ensures the survival of the fittest piglets when conditions are poor (Fraser *et al.* 1995). Consequently, long and variable birth intervals are not easily reconcilable with poor maternal behaviour. The exception being when long and variable birth intervals do not simply promote competitive asymmetry but result in a reduction in the viability of the litter as a whole.

The first milk and colostrum the piglet receives is obtained freely, without the need for teat massage (Castren *et al.*, 1992). However, a regular pattern to the milk letdowns soon develops and milk is then only available during short periods and at all teats at the same time (Fraser, 1980; Ellendorff *et al.*, 1982; Castren *et al.*, 1992). As a pattern to the milk letdowns develops, piglets develop a suckling rhythm and the behaviour of the litter becomes synchronised (Lewis and Hurnik, 1985; de Passille and Rushen, 1989). Thus, the percentage of piglets suckling at the udder at the same time increases over the first week following birth, except for litters prone to mortality (de Passille and Rushen, 1989). Staying at the udder in between milk letdowns can be a dangerous strategy for piglets (Weary *et al.*, 1996b). However, small piglets that are not competing well for their mothers milk may gain benefits by

remaining at the udder. Actively massaging a teat between milk letdowns can result in that teat becoming more productive (Fraser, 1984; Algers and Jensen, 1985). In addition, staying attached to a teat gives the piglet a residents advantage over other piglets trying to displace it (Fraser *et al.*, 1995).

Sows, aiming to maximise their reproductive success, must trade-off the relative risks and benefits of how best to organise their behaviour. One of these trade-offs concerns how often a sow stands up throughout lactation. Standing up is necessary to gain access to food and water, which is required to maintain milk output, but by doing so the sow risks crushing her piglets when she lies back down again (e.g. Edwards *et al.*, 1986; Weary *et al.*, 1996a). The most adaptive strategy will depend on many factors, such as how careful the sow is when she lies down, litter size, how much space she has to manoeuvre and whether she can see all around her.

Much has been written about the higher litter sizes (e.g. Bidanel *et al.*, 1989) and nutrient rich milk (e.g. Zou *et al.*, 1992) of Meishan sows and gilts compared to standard European breeds. However, there is less information about how the maternal behaviour of the Meishan breed differs from that of the standard European breeds. Meunier-Salaun *et al.* (1991) found few behavioural differences between Meishan and Large White sows during 24 hours following the onset of parturition but report that Meishan piglets were more likely to rest at the udder than Large White piglets. In contrast, Sinclair *et al.* (1996) reported that Meishan synthetic (50% Meishan) sows were more docile during lactation and had shorter intervals between milk letdowns than Landrace and Large White sows. Cross-fostering experiments have shown that Meishan sows have better piglet survival than Landrace sows (van der Steen and de Groot, 1992). Therefore, there is interest in whether these maternal qualities in the rearing ability of the Meishan breed can be incorporated into commercial genotypes for the European market.

Breed differences for breeds reared identically, provide a basic indication of genetic variation in a trait but more importantly, variation that might be exploited by manufacturing various synthetic breeds. Additional circumstantial evidence of

genetic influences on behaviour is gained by studying consistency in the expression of a behaviour over subsequent parities (Simm, 1998). The current study identifies the behavioural differences between Meishan pure, Meishan-Landrace, Landrace-Duroc and Duroc breeds, that are present following the onset of the parturition.

In contrast to the Meishan pure, the Duroc pure is not known for its maternal quality. The Duroc breed used in this study has not been the focus of any artificial selection for litter size in recent years (Dr. A. D. Hall, Cotswold Pig Development Company, pers. comm.). Therefore, comparisons between Duroc and the other breeds not only represent fundamental genotypic differences but also the effect artificial selection for litter size has had on other traits.

The aim of this study was to further understand the biology of maternal behaviour following the onset of parturition. Principally, breed differences, consistency and change over the first two parities and the effect of straw in the farrowing crate.

Experimental Design

The experiment was based around a breed by parity by treatment factorial design. Four breeds were studied, Meishan pure, Meishan-Landrace synthetic, Landrace-Duroc synthetic and Duroc pure, with sows observed over two parities. The design was unbalanced largely because of sows 'dropping out' between parities (see Chapter 2). All sows and gilts farrowed in crates of two different designs (see Chapter 2). Treatment was the presence or absence of straw that was allocated randomly within breeds (see Chapter 2).

Behavioural Observations

Sows and gilts were observed from the birth of the first piglet (BFP) for six hours continuously and then for a further six 10-minute samples at 9, 12, 15, 18, 21 and 24 hours (see Chapter 2). The behaviour of sows and gilts over time was summarised as fourteen 30-minute time intervals, twelve from the six hour sample and two from collating information from samples and 9, 12 and 15 hours and from samples at 18, 21 and 24 hours. The behaviours recorded are described in the ethogram (see Chapter 2, Tables 2.6 and 2.7.

Piglet behaviour and location was measured on a whole litter basis using scan samples every 5 minutes during the sow observation times (see Chapter 2, Table 2.8). Change in piglet behaviour and location over time was summarised as seven 60-minute time intervals, six from the six hour time sample and one from collating 10-minute samples at 9, 12, 15, 18, 21 and 24 hours. The 60-minute interval was chosen to summarise the piglet scan samples because this time interval contained 12 scan

samples, which was greater than the number of piglet behaviour and location categories.

Statistical Analysis

Behaviours measured as frequencies (events) were transformed to the logarithmic scale, and behaviours measured as proportions (states) were transformed using the arcsine-square-root transformation. These transformations succeeded in making most of the behavioural measures fit the requirements of parametric tests. Post-hoc analysis of residuals and fitted values were used to check whether the data fulfilled parametric criterion.

Measures that failed to reach parametric criterion, usually due to the behaviours being rare and infrequent, were not analysed. In a few cases rare and infrequent behaviours would fulfil parametric criterion after collating all time samples together so that one value per sow-parity was created. In these cases, it was impossible to assess changes over time, within a parity, in the expression of these infrequent behaviours.

Sow-piglet interactions, nose, touch, root, snap and bite, were incorporated into a sow responsiveness index as "responses". This index was designed to control for between litter differences in the frequency with which a given sow would come into head to head contact with her piglets. This index was adapted from Jarvis (1997).

$$\text{Responsiveness} = \frac{\text{response} - \text{no response}}{\text{response} + \text{no response}}$$

Where, response = sum of the frequencies of nose, touch, root, snap and bite
and, no response = frequency with which a piglet comes within one bodylength of the sows head and the sow does not interact with the piglet

Thus, an index score of: +1 = all response

-1 = all no response

Restricted Maximum Likelihood Tests (Genstat, Version 5, Release 4.1, 1998, Lawes Agricultural Trust) were used for the analysis of sow behaviour, frequencies of different posture changes and piglet behaviour and location data. This statistical procedure acted like a mixed model with fixed and random effects. The fixed effects specified were breed, parity and treatment and all factors and co-variates listed in Table 4.1. The random effects specified described the structure of the data, i.e. sow nested within parity nested within time (sow/parity/time).

Fixed effects with non-significant Wald statistics (Chi-squared distribution) were dropped from the model. All possible factor interactions were explored and included in the final model if they had significant Wald statistics. The factor of interest was always fitted last in the REML model, thereby controlling for all other factors and co-variates in the model. Differences between different levels within a factor were identified using the REML estimates and the standard error of the mean to calculate t-statistics. Means were quoted with either their standard error, if a transformed value was analysed, or their 95% confidence interval, if values were back-transformed.

The random effects structure of the mixed REML model split the sample variance into three strata: 'sow' (between sows), 'sow.parity' (within sows, between parities) and 'sow.parity.time' (within sow-parity, between time samples). The 'sow' and 'sow.parity' stratum variances were used in F-tests (variance ratio tests) to estimate the degree of individual consistency between parities one and two. Consistency was defined as the tendency of an individual to express similar levels (frequency or time spent) of a particular behaviour during two subsequent farrowings. Since stratum variances were used, this measure of behavioural consistency was based on the REML-estimated fitted values adjusted to all the terms in the model.

Table 4.1: Non-experimental factors included in the statistical model, if they had a significant effect. All of these factors represent potential, measured sources of variation between litters.

Factor	Description
BFP Time	Time of day when parturition began. Four levels, see Chapter 3.
Season	Time of year of parturition. Four levels, see Chapter 3.
Age of sow	Age of sow at parturition (min = 256 days, max = 856 days). Largely confounded with parity. Five levels, see Chapter 3. Also fitted as a co-variate.
Ease of movement	Score based on how difficult it was moving the sow from gestation pen to farrowing crate. Scored from 1 to 5 (see Chapter 2 for definitions, Chapter 3 for sample sizes).
Farrowing house	Which farrowing house the sow farrowed in. Old (n = 121) versus new (n = 38) (see Chapter 2 for descriptions).
Radio	Whether or not a radio was playing in the farrowing house at the time the sow was farrowing. Yes (n = 117), no (n = 42).
Cross-fostering	Whether or not cross-fostering occurred, how many piglets were fostered and whether these were on or off the sow. Five levels: 1. No cross-fostering occurred (n = 106) 2. Two or fewer piglets were fostered off (n = 24) 3. Three or more piglets were fostered off (n = 23) 4. Two or fewer piglets were fostered on (n = 28) 5. Three or more piglets were fostered on (n = 28)
Length of parturition	1. <65 minutes (n = 5) 2. 65-120 minutes (n = 34) 3. 125-180 minutes (n = 37) 4. 185-240 minutes (n = 30) 5. 245-300 minutes (n = 18) 6. 305-360 minutes (n = 10) 7. >360 minutes (n = 25)
Litter size	Litter size was included as a factor with three levels: 1. Less than eight (n = 17) 2. Between eight and twelve piglets (n = 91) 3. Thirteen or more piglets (n = 50)
Drugs	Whether or not drugs (e.g. oxytocin, "Stresnil", antibiotics) were given to the sow or gilt during farrowing. Two levels, yes (n = 13) or no (n = 146)
Days in crate prior to BFP	Variation between litters in the length of time the sow or gilt was in the crate prior to the onset of parturition. Six levels, see Chapter 3.
Length of sow	Length of sow, as estimated from the video screen (see Chapter 2), was fitted as a co-variate.

Length of Parturition, Litter size and Birth Intervals

a) Length of Parturition

Length of parturition was measured from the birth of the first piglet until the first expulsion of placental membranes following the birth of the last piglet. Length of parturition was measured to the nearest five minutes, recorded during the five minute piglet scan samples.

Sows were not consistent over parities one and two in the time taken to complete parturition. There were no parity or age effects and no effect of straw on the length of parturition. However there were strong breed differences in the length of parturition. Duroc sows had significantly longer parturitions (289 +/- 11 minutes) than either Landrace-Duroc (216 +/- 21 minutes; $t_{69} = 3.2$, $p<0.01$), Meishan-Landrace (160 +/- 11 minutes; $t_{124} = 8.1$, $p<0.001$) or pure-bred Meishan (168 +/- 21 minutes; $t_{70} = 5.3$, $p<0.001$). Whilst Landrace-Duroc sows had longer parturitions than Meishan-Landrace ($t_{85} = 2.4$, $p<0.02$).

Litter size also had a big effect on length of parturition. Sows having 13 or more piglets took longer to complete parturition (259 +/- 19 minutes) than sows having between 8 and 12 piglets (199 +/- 14 minutes; $t_{140} = 4.2$, $p<0.001$) or less than 8 piglets (167 +/- 23 minutes; $t_{65} = 4.1$, $p<0.001$). The lengths of parturition for small (less than 8) and medium sized litters (8 - 12) were not significantly different.

b) Litter Size

Mean litter size (including still-births) was affected by parity with sows in their second parity having significantly more piglets born (12.3 +/- 0.3 piglets) than parity one gilts (11.1 +/- 0.3 piglets; $t_{157} = 3.5$, $p<0.001$).

Litter size also varied between the breeds. Duroc litters were smaller (10.5 +/- 0.3 piglets) than either Landrace-Duroc (11.8 +/- 0.4 piglets; $t_{69} = 2.2$, $p<0.05$), Meishan-Landrace (11.5 +/- 0.3; $t_{124} = 2.5$, $p<0.02$) or pure-bred Meishan litters (13.0 +/- 0.4 piglets; $t_{70} = 4.1$, $p<0.001$). In addition, the litters of pure-bred Meishan gilts were significantly larger than the litters of Meishan-Landrace sows and gilts ($t_{86} = 2.4$, $p<0.02$) but not larger than those of Landrace-Duroc sows and gilts ($p<0.10$).

c) Birth Intervals

Each sow had two values, in addition to the length of parturition and litter size, which described the progress of parturition. These were mean birth interval and the standard deviation in mean birth interval.

Mean birth interval, and the standard deviation for mean birth interval, had to be square-root transformed to fit parametric criterion. One outlier was removed, which was a Meishan gilt that had the majority of her parturition assisted by the farm staff. This gilt had a parturition longer than the maximum parturition length category of 360 minutes so could be still included in the length of parturition analysis.

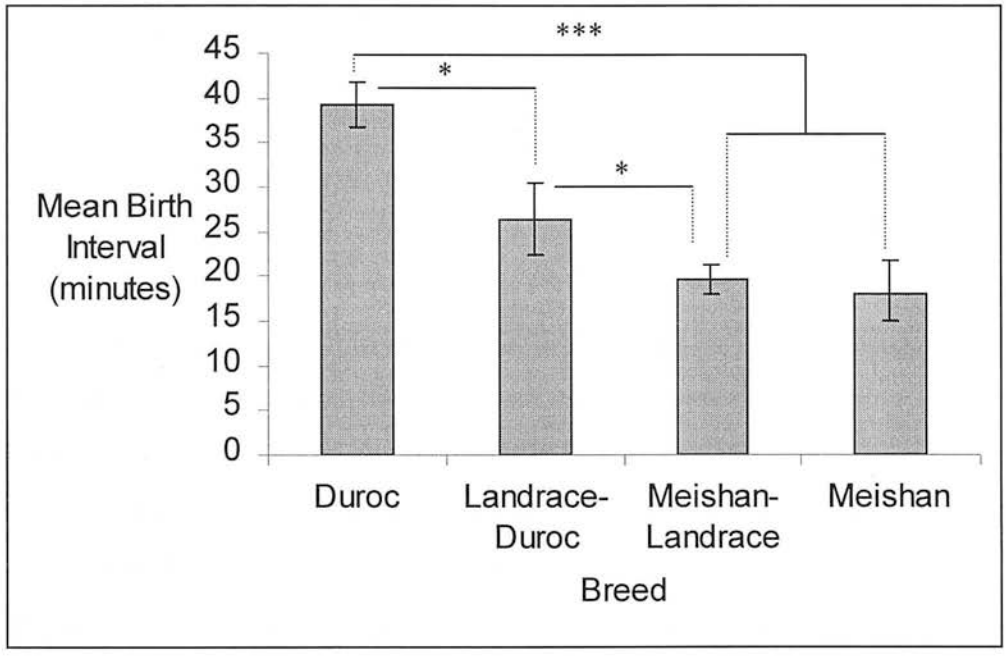
There was no overall effect of parity on mean birth interval or the standard deviation of mean birth interval. In addition, individual sows did not show any consistency in their mean birth interval or the standard deviation of mean birth interval between the first two parities.

The presence of straw did not effect mean birth interval or the standard deviation of mean birth interval.

Mean birth intervals were significantly longer for Duroc sows (39.2 +/- minutes) than either Landrace-Duroc (26.3 +/- minutes; $t_{69} = 2.3$, $p<0.05$), Meishan-Landrace (19.7 +/- minutes; $t_{124} = 6.4$, $p<0.001$) or pure-bred Meishan (18.1 +/- minutes; $t_{70} = 5.3$, $p<0.001$). Whilst Landrace-Duroc sows had longer birth intervals than pure-bred

Meishan (t_{36} = 2.3, $p<0.05$) and Meishan-Landrace sows (t_{85} = 2.3, $p<0.05$) (see Figure 4.1). In addition, the standard deviation in mean birth interval was larger for Duroc (28.2 minutes, 95% CI = 25.4 - 35.0) than for Meishan (11.8 minutes, 95% CI = 8.9 - 15.1; t_{70} = 3.9, $p<0.001$) or Meishan-Landrace sows and gilts (13.3 minutes, 95% CI = 11.7 - 15.1; t_{124} = 4.7, $p<0.001$). The birth intervals of Landrace-Duroc sows and gilts (22.1 minutes, 95% CI = 18.1 - 26.5) were more variable than Meishan-Landrace sows and gilts (t_{124} = 2.2, $p<0.05$) and tended to be more variable than Meishan gilts (t_{31} = 2.0, $p<0.10$).

Figure 4.1: Breed differences in Mean Birth Interval (+/- 95% confidence interval). Values are back-transformed REML estimates, controlled for repeated measures, age of sow, parity, season and whether drugs were given but not litter size. See text for details.
* = $p<0.05$, *** = $p<0.001$



There was also a small litter size effect on mean birth interval but this interacted with season (W_6 = 14.8, $p<0.05$). (see Table 4.2). During Spring (March - May) farrowings, litters of seven or fewer piglets had longer mean birth intervals than litters of between eight and 12 litters (t_{106} = 3.17, $p<0.01$) and litters of thirteen or more litters (t_{65} = 2.23, $p<0.05$).

Table 4.2: Differences between small, medium and large litters, per season, in the mean birth interval (minutes). Values are back-transformed REML estimates, controlled for repeated measures, parity, breed, season, age of sow and whether drugs were administered to the sow or gilt. Values in brackets are the 95% confidence intervals. Means that differ significantly at $p<0.05$, between litter sizes and within seasons, have different superscripts.

Mean Birth Interval (minutes) (plus 95% confidence interval)			
Time of year	**7 or fewer piglets**	**8-12 piglets**	**13 or more piglets**
Dec-Feb	29.0^{a} (22.3 - 36.6)	20.8^{a} (18.9 - 22.7)	26.8^{a} (22.9 - 30.9)
Mar-May	43.9^{a} (35.5 - 53.1)	22.3^{b} (20.4 - 24.3)	24.1^{b} (20.4 - 28.0)
Jun-Aug	21.1^{a} (15.5 - 27.7)	22.3^{a} (20.4 - 24.3)	29.0^{a} (25.0 - 33.3)
Sep-Nov	21.3^{a} (15.6 - 27.9)	20.9^{a} (19.1 - 22.9)	24.7^{a} (21.0 - 28.7)

The management decision to administer drugs to a sow or gilt during parturition was associated with the mean birth interval. Sows given drugs during parturition had marginally longer mean birth intervals (28.7 minutes, 95% confidence interval (CI) = 25.3 - 32.3) than for sows not given drugs (21.9 minutes, 95% CI = 21.0 - 22.8; Wald, $\chi^2 = 4.0$, d.f. = 1, $p<0.05$). The type of drug administered, and when it was administered, is likely to affect the behaviour recorded. For example, oxytocin was given to five gilts and three sows, sometimes during parturition and sometimes after parturition; "Stresnil", a drug given to active or aggressive sows and gilts, was given to four gilts, one before farrowing, two on the day of parturition and one the day after parturition. In addition, antibiotics were sometimes given to sows and gilts especially if parturitions were assisted. Drug administration occurred too infrequently to model the effects of different drugs and when they were administered, so the average effect

of these drugs on the behaviour of sows was used to control for the effect of drug administration on sow and gilt behaviour.

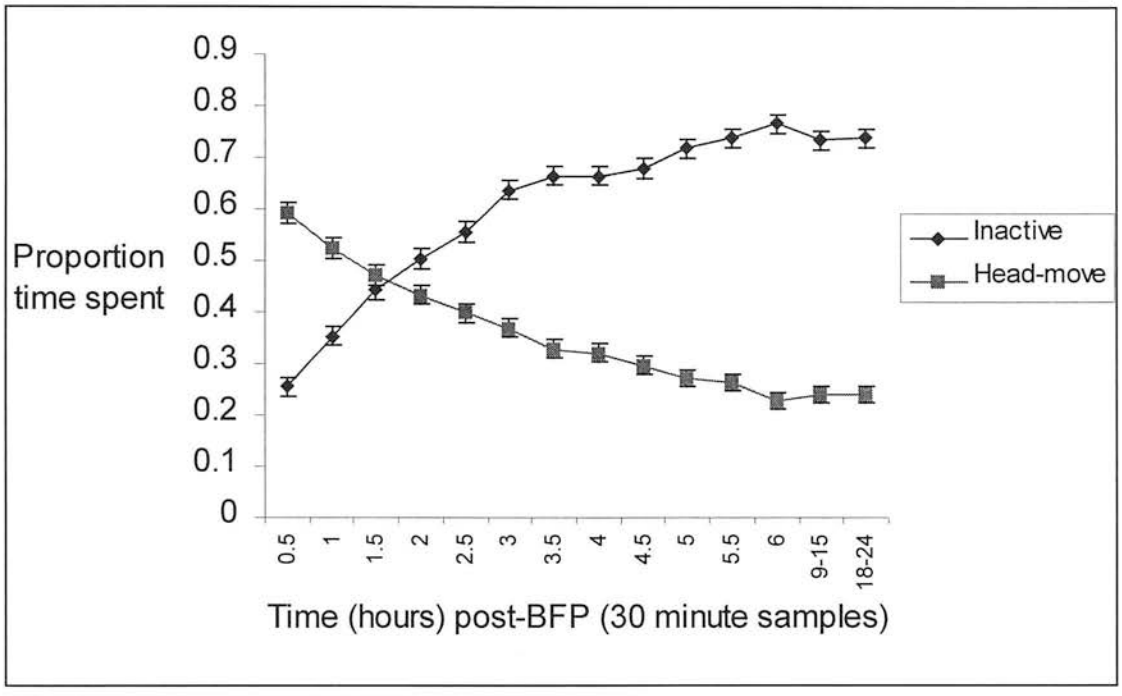
Sow and Piglet Behaviour

Changes in Behaviour over Time

Sow Behaviour

Sow activity decreased over the 6 hours following the onset of parturition (hereafter known as the birth of first piglet or BFP) (see Figure 4.2). Time spent inactivity, or in a general state of alertness ('head-move') were not significantly different between 9 and 24 hours post-BFP than those seen at the end of the first 6 hour sample.

Figure 4.2: Changes over time following the onset of parturition (BFP) for the time sows spend inactive and time sows spend in a state of general alertness ('head-move') (+/- 95% confidence intervals). Values are back-transformed REML estimates adjusted for repeated measures, breed, parity and treatment differences and all factors listed in Table 4.1.

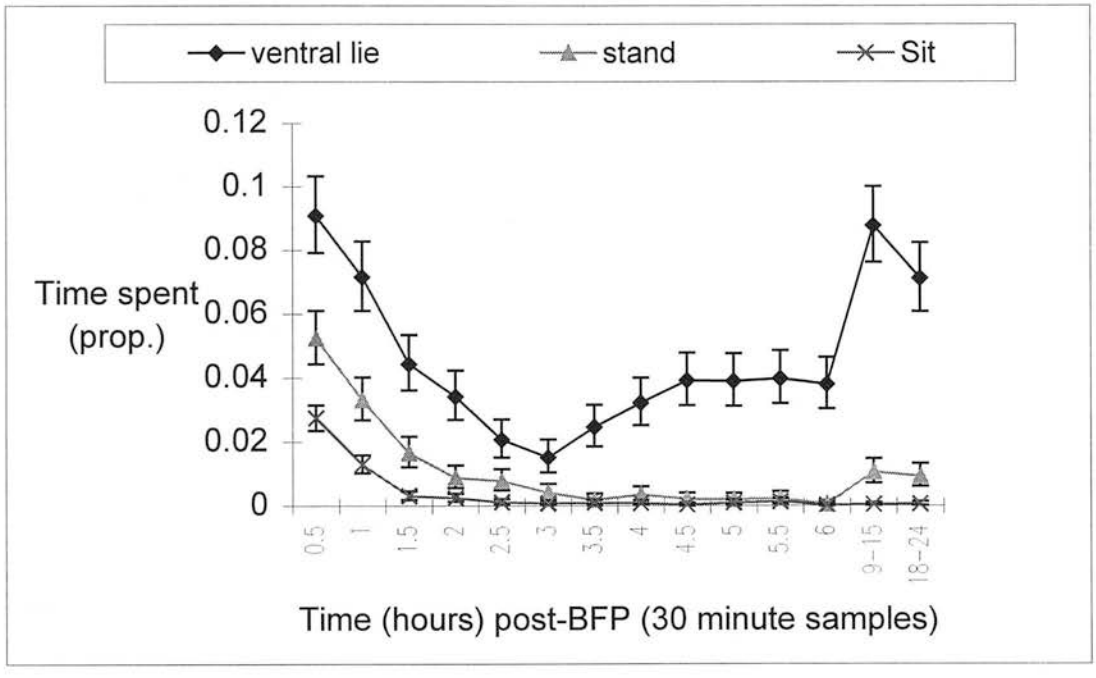


Time spent engaged in straw or floor directed behaviour was highest during the first hour post-BFP (5.2%, 95% CI = 4.8 - 5.6%), was significantly lower during the second hour (1.0%, 95% CI = 0.9 - 1.2%; $t_{157} = 10.2$, $p<0.001$) and lower again in the third hour (0.5%, 95% CI = 0.3 - 0.6%; $t_{157} = 2.80$, $p<0.01$). Thereafter, very little time is spent interacting with the straw or floor.

Time spent lying laterally increased rapidly following the birth of the first piglet (66.0%, 95% C.I. = 63.4 - 68.5%, first 30 minute sample) until 3 hours post-BFP (93.8%, 95% C.I. = 92.4 - 95.0%, fifth 30 minute sample; $t_{157} = 10.8$, $p<0.001$). Subsequently, time spent lateral lying remained at this high level until the end of the 6-hour sample. During the samples from 9 to 24 hours post-BFP, sows spent significantly less time lying laterally (83.5%, 95% C.I. = 81.4 - 85.4%) than that seen between 2 and 6 hours post-BFP ($t_{157} = 4.0$, $p<0.001$).

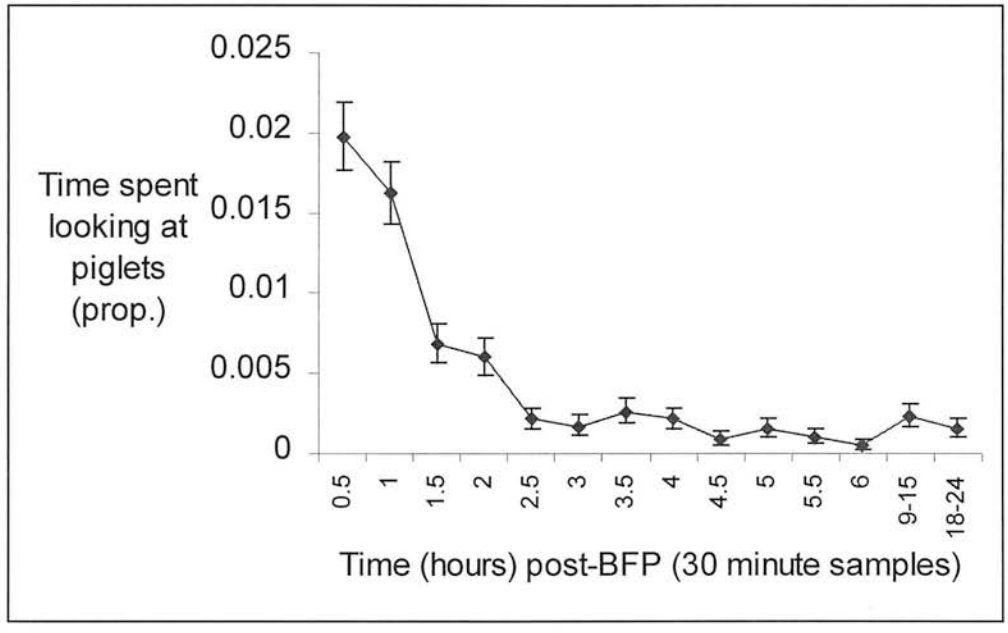
Time spent lying ventrally, standing and sitting is shown in Figure 4.3. During the first 3 hours following BFP, time spent in these postures decreased as time spent in the lateral lying posture increased. Sows and gilts spent more time ventral lying (t_{157} = 3.5, $p<0.001$) and standing (t_{157} = 3.04, $p<0.01$) during the 9 to 24-hour samples, than during most of the first six hours (see Figure 4.3).

Figure 4.3: Changes over time following the onset of parturition (BFP) for time spent lying ventrally, standing and sitting (+/- 95% confidence intervals). Values are back-transformed REML estimates adjusted for repeated measures, breed, parity and treatment differences and all factors listed in Table 4.1.



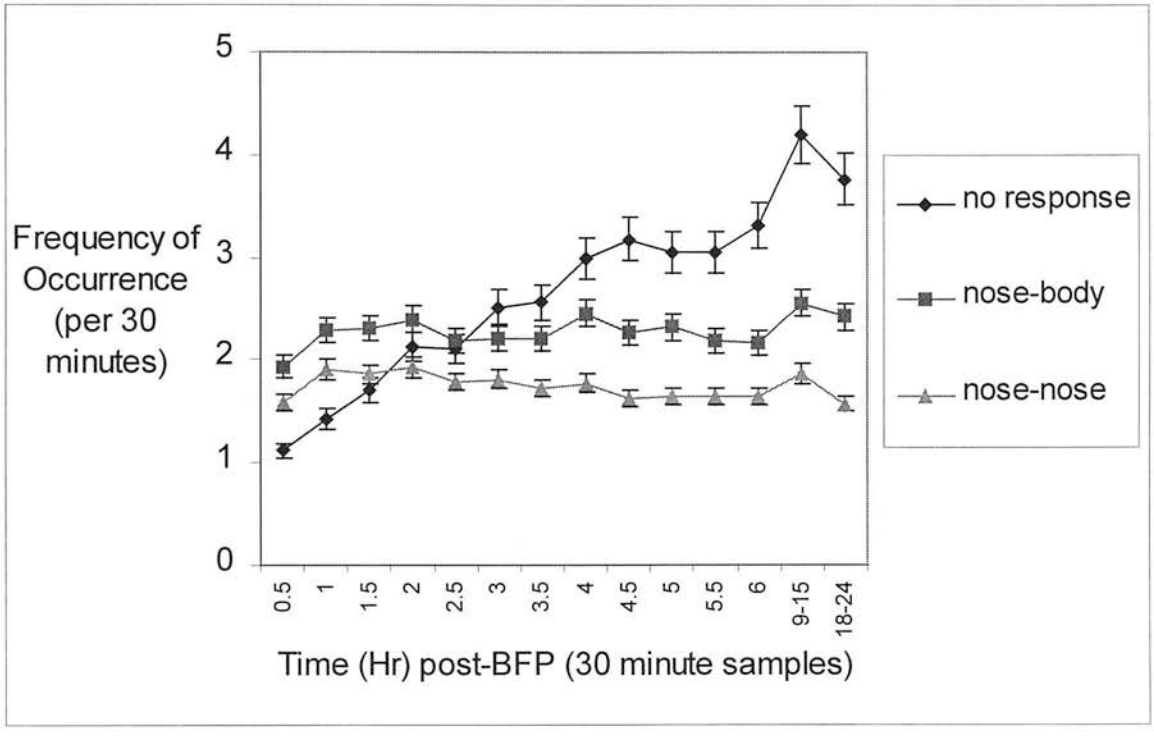
Time spent looking at piglets was highest during the first 30 minutes following the first birth and decreased over the following two hours (t_{157} = 5.9, p<0.001) (see Figure 4.4). Thereafter time spent looking at piglets did not change over the rest of the observation period (see Figure 4.4).

Figure 4.4: Changes over time following the onset of parturition (BFP) in the time sows spent looking at piglets in their litter (+/- 95% confidence intervals). Values are back-transformed REML estimates adjusted for repeated measures, breed, parity and treatment differences and all factors listed in Table 4.1.



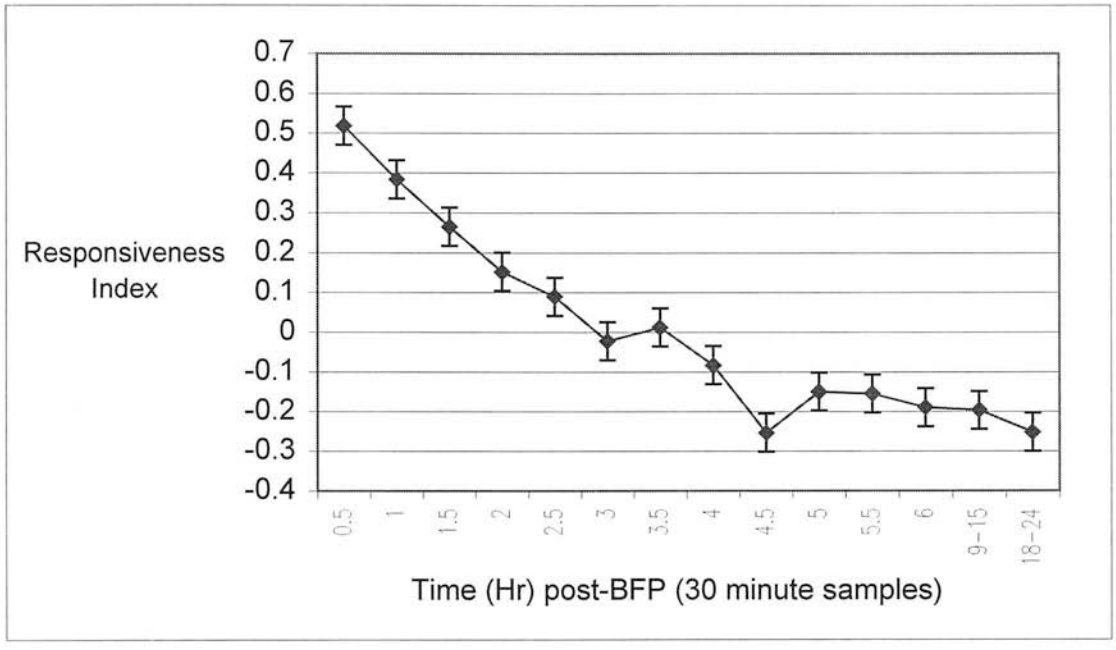
Frequencies of nose to nose and nose to body sow-piglet contacts were relatively constant over time during the first 24-hours (see Figure 4.5). In contrast, there was a strong time effect on the frequency with which a sow would not respond to a piglet coming within one body length of her head ('no response') (Wald, χ^2 = 592, d.f. = 13, p<0.001) (see Figure 4.5).

Figure 4.5: Mean frequency (+/- 95% confidence interval) of occurrence of nose to nose and nose to body sow-piglet interactions, and the mean frequency of not responding to piglets, following the onset of parturition (BFP). Sample points represent 30 minutes of behavioural observation. Frequencies are back-transformed REML estimates, adjusted for repeated measures, breed, parity and treatment differences and all factors listed in Table 4.1.



The responsiveness index reflected the changes over time in the frequency of sow-piglet interactions and not responding to piglets (Figure 4.6). There was a strong time period effect on the responsiveness of sows following the onset of parturition (Wald, χ^2 = 352.9, d.f. = 13, $p<0.001$). Responsiveness decreased from the onset of parturition (BFP) until the fourth hour post-BFP. Thereafter, sow responsiveness does not change over subsequent time samples (see Figure 4.6).

Figure 4.7: Changes over time in the responsiveness of sows to their piglets (+/- standard error) (see Methods for definition of responsiveness). The values presented are REML estimates adjusted for repeated measures.



Piglet Location and Behaviour

Piglet behaviour and location, as measured by scan samples of the litter as a whole, also changed over time during the first 24 hours of life.

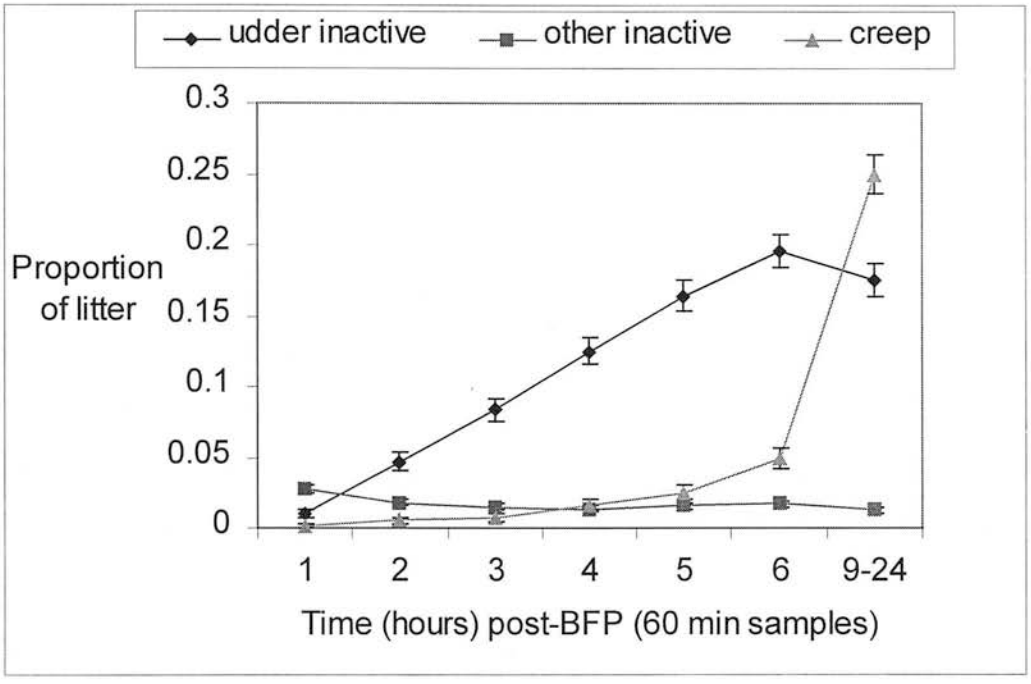
The proportion of the litter found close to the sows head was highest during the first hour (3.9%, 95% CI = 3.6 - 4.3%), significantly lower in the second hour (2.6%, 95% CI = 2.3 - 2.9%; $t_{157} = 3.0$, $p<0.01$) and lower again in the third hour (1.5%, 95% CI = 1.3 - 1.7%; $t_{157} = 3.2$, $p<0.01$). Thereafter the proportion of the litter found close to the sows head per hour did not change.

Litters increased the time spent active at the udder (i.e. massaging udder and suckling) from the first hour (19.2%, 95% CI = 17.8 - 20.7%) to the second hour

(39.1%, 95% CI = 37.3 - 40.9%; $t_{157} = 8.4$, $p<0.001$) and then again for the third hour post-BFP (46.3%, 95% CI = 44.4 - 48.2%; $t_{157} = 2.7$, $p<0.01$). The proportion of time litters spent active at the udder remained constant for the remainder of the six hour observation period. During the 9 to 24 hour time samples, the proportion of time litters spent active at the udder was lower (25.0%, 95% CI = 23.4 - 26.7%) than that seen at the end of the 6 hour post-BFP sample (38.1%, 95% CI = 36.3 - 39.0%; $t_{157} = 5.4$, $p<0.001$).

The proportion of time litters spent inactive at the udder (i.e. resting, sleeping) increased from the birth of the first piglet (BFP) until six hours post-BFP (Wald, $\chi^2 = 796.8$, d.f. = 6, $p<0.001$) (see Figure 4.7). During the time samples between 9 and 24 hours, time spent inactive at the udder was not significantly different from what was recorded at the end of the six hour sample (see Figure 4.7).

Figure 4.7: Proportion of a litter found (a) inactive the sows udder, (b) inactive away from the sow or creep ('other inactive') and (c) in the creep following the birth of the first piglet. Values are back-transformed REML estimates adjusted for repeated measures on the sow, breed, parity and treatment effects, and all factors listed in Table 4.1.



Time spent in the creep increased from approximately three hours following the onset of parturition until six hours post-BFP (t_{157} = 6.01, p<0.001) (see Figure 4.7). During the time samples 9 to 24-hours, the proportion of the litter in the creep was much higher than the proportion in the creep six hours post-BFP (t_{157} = 13.2, p<0.001) (see Figure 4.7).

Inactivity away from the sow or creep was highest in the first hour following the onset of parturition (t_{157} = 2.6, p<0.02) and then remained relatively constant for the rest of the sample time (see Figure 4.7).

The time a litter spent active away from the sow or creep area was highest during the first hour (26.7%, 95% CI = 25.9 - 27.6%), significantly lower in the second hour (17.3%, 95% CI = 16.6 - 18.0%; t_{157} = 8.5, p<0.001) and lower again in the third

hour 13.4%, 95% CI = 12.8 - 14.1%; t_{157} = 3.9, $p<0.001$). Time spent active away from the sow or creep decreased again between the third and sixth hours (11.2%, 95% CI = 10.6 - 11.8%; t_{157} = 2.6, $p<0.02$). Time spent active away from the sow or creep was much lower during the 9 to 24 hour time samples (7.9%, 95% CI = 7.4 - 8.4%) compared to that seen at the end of the six hour time period (t_{157} = 4.2, $p<0.001$).

Consistent Behavioural Traits Over Parities One and Two

The consistency analysis based on the stratum variance ratio tests identified a significant sow component in approximately 50% of the behaviours analysed. These behaviours and their stratum variances are summarised Table 4.2. Behaviours that did not show individual consistency were: inactive, headmove, look at piglets, lateral lie, sitting, standing, stepping, backing up against the crate, and the following posture changes – lying down to a lateral lying posture, lie to sit, sit to lie and changing lying postures.

The expression of sow-piglet interactions showed a high degree of consistency within individual sows over parities one and two. Nose to nose contacts ($F_{89,47}$ = 2.2, $p<0.005$), nose to body contacts ($F_{96,51}$ = 3.2, $p<0.001$) and the frequency of 'no responses' ($F_{88,44}$ = 2.3, $p<0.002$) all showed consistency of expression between parities one and two. Similarly, the responsiveness index (see Methods), which incorporated all sow-piglet interactions, was also consistent within individuals across parities ($F_{93,50}$ = 2.34, $p<0.002$). Figure 4.8 shows the relationship between parity one and parity two values of nose to nose and nose to body sow-piglet interactions for all 57 sows that were observed over two parities. Note that these graphs display the original raw data, whereas the consistency analysis was based on REML-estimated fitted values.

The biting of piglets (events whereby the piglet ends up in the sow's mouth) occurred too infrequently to be analysed, even over a 24 hour period. However, attempted bites (events where the piglet did not end up in the sow's mouth) could be analysed

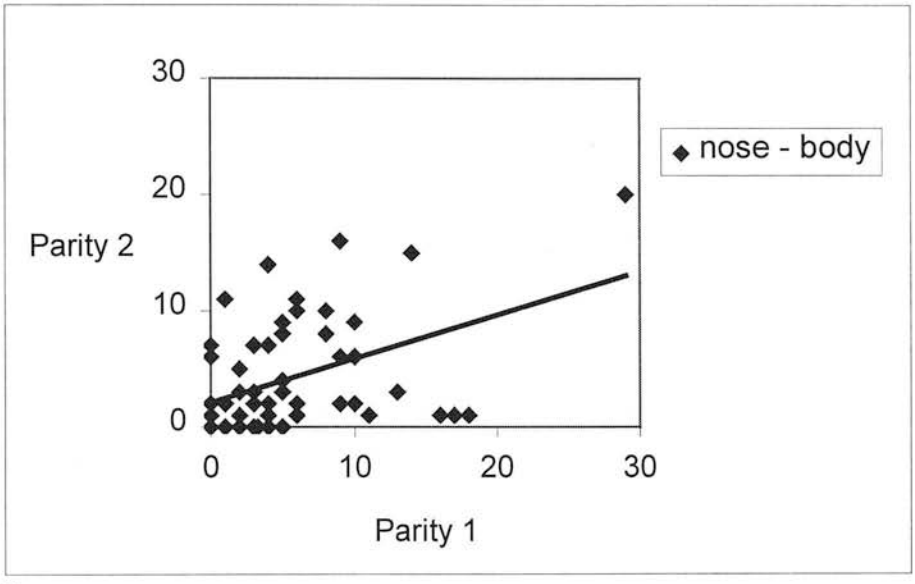
by collating all time samples within a parity. There was some evidence of consistency between parities one and two in the frequency with which individual sows snapped at piglets ($F_{92, 51} = 1.9$, $p<0.02$). The frequency of rooting piglets (pushing with the snout) was also consistent within individuals across parities ($F_{93, 49} = 2.3$, $p<0.01$).

Table 4.2: F-ratio tests on the random model stratum variances. The ratio Sow:Sow.parity gives a value on the F-distribution. High variance in the sow stratum compared to the sow.parity stratum indicates consistency in the expression of a behaviour within individual sows between parities one and two. This consistency is based on the REML-estimated fitted values for each behaviour, and is thus adjusted for all other terms in the model. The top twelve behaviours are measures taken from the sow, the bottom two behaviours are measures of piglet behaviour and location. Behaviours are defined in the ethograms, Tables 2.6 and 2.7 (Chapter 2).

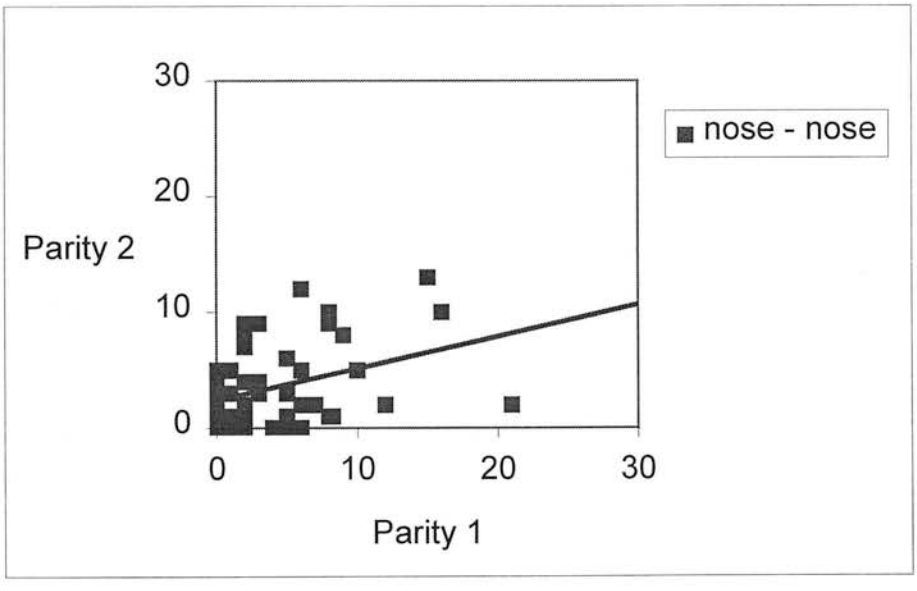
Behaviour	**Stratum Variances**		**F-test**
	Sow	Sow.parity	**p-value**
Nose-nose ('nose')	0.240	0.107	<0.005
Nose-body ('touch')	0.413	0.127	<0.001
Snap (attempted bite)	0.089	0.048	<0.02
Root (push away with snout)	0.156	0.069	<0.01
No response	0.605	0.258	<0.002
Responsiveness	1.394	0.595	<0.002
Straw/Floor-directed behaviour	0.048	0.029	<0.05
Ventral Lie	0.428	0.220	<0.02
Stand-kneel	0.116	0.052	<0.001
Kneel-lie	0.109	0.046	<0.001
Lie-stand	0.064	0.039	<0.05
Sit-stand	0.089	0.049	<0.05
Proportion of the litter inactive and away from the sow or creep	0.052	0.020	<0.001
Proportion of the litter at the sows vulva	0.005	0.003	<0.05

Figure 4.8: Frequencies of (a) nose to body and (b) nose to nose sow-piglet interactions per sow (n = 57) over parities one and two (raw data). The stratum variance ratio analysis from the fitted REML mixed model (Table 4.2) indicated consistency (based on REML fitted values) in sow behaviour between parities one and two ($p<0.001$ and $p<0.005$ respectively). The trend lines on each graph are calculated using linear regression (Microsoft Excel).

(a)



(b)



In addition to the sow-piglet interactions, time spent lying ventrally ($F_{94,54}$ = 1.9, $p<0.02$) and time spent interacting with the straw or floor of the crate ($F_{96,58}$ = 1.7, $p<0.05$) showed some evidence of consistency within sows, over parities one and two.

Time spent inactive, alert (head move), looking at piglets, lying laterally, sitting, standing and frequencies of stepping and pushing against the back of the crate were not consistent within individuals between parities one and two.

In the analyses of sow posture changes, two posture changes showed strong consistency between parity, stand-kneel ($F_{99,57}$ = 2.22, $p<0.001$) and kneel-lie ($F_{99,56}$ = 2.39, $p<0.001$), and two showed weak consistency between parities, lie-stand ($F_{97,60}$ = 1.67, $p<0.05$) and sit-stand ($F_{95,58}$ = 1.83, $p<0.05$). Other posture changes (lie-sit, sit-lie, changing posture whilst lying and lying down to a lateral lying posture did not show intra-individual consistency between parities.

The behaviour and location of sow litters over time were consistent between parities one and two in the proportion of the litter found at the sows vulva and the proportion of the litter inactive away from the sow and creep. All other measures of piglet behaviour and location were not consistent within sow litters between parities.

Change Over Parities One and Two and Age Effects

Effects of parity were largely confounded by age but some overlap existed for the middle age group (see Table 4.7). The REML model was unable to separate effects of age from effects of parity since all parity effects disappeared if age was specified earlier in the model, and vice versa for effects of age. Thus age effects on behaviour were studied within parity and parity effects are reported without controlling for age.

Table 4.3: Sample sizes for the different parity and age combinations

	Age of Sow (days)				
	256-355	**356-455**	**456-555**	**556-655**	**>655**
Parity 1	24	64	8	0	0
Parity 2	0	0	23	35	5

a) Parity Effects

There were only three behavioural differences between the behaviour of parity one gilts and parity two sows and their litters, these are summarised in Table 4.4.

Table 4.4: Differences between the behaviour of parity one gilts and parity two sows and their litters. Values are back-transformed REML estimates controlled for repeated measures, breed, treatment and all factors listed in Table 4.1 except age of sow.

Behaviour	**Parity**		**Wald, χ^2, d.f. = 1, p-value**
	1	**2**	
Ventral lie (time spent)	5.79% (5.03 - 6.60%)	2.40% (1.81 - 3.08%)	p<0.01
Changing lie postures (freq. per hour)	2.30 (2.18 - 2.42)	1.80 (1.68 - 1.92)	p<0.01
Use of the creep within litters	4.31% (3.80 - 4.85%)	2.34% (1.88 - 2.85%)	p<0.01

Parity one gilts spent more time lying ventrally than parity two sows (Wald, χ^2 = 10.7, d.f. = 1, p<0.01), but without spending any less time in any other single posture. Changing lie postures was seen more frequently in parity one gilts than

parity two sows (Wald, $\chi^2 = 8.3$, d.f. = 1, $p<0.01$), whilst other types of posture change were not affected by parity.

The litters of parity one gilts spent more time in the creep than the litters of parity two sows (Wald, $\chi^2 = 7.4$, d.f. = 1, $p<0.01$), but without spending less time in an alternative piglet behaviour and location category.

b) Effects of Age within Parity

The effect of age, within a parity, on the behavioural time budgets of sow and gilts was analysed first using age as a co-variate and then by dividing age into the categories shown in Table 4.5.

Age commonly co-varied with the behaviour of parity one gilts but only rarely with the behaviour of parity two sows (see Table 4.5). Thus, during parity one, age positively co-varied with inactivity and time spent in a lateral lie posture; and negatively co-varied with the frequency of stepping, time spent looking at piglets and time spent in a ventral lie posture. In parity two, age of sow weakly co-varied with time spent in the head-move behaviour (positively) and time spent inactive (negatively) (see the regression estimates in Table 4.5). Age effects on time spent lying ventrally are displayed in Figure 4.9.

Figure 4.9: Parity-dependent age effects on time spent lying ventrally (+/- 95% confidence intervals). Values are back-transformed REML estimates (95% confidence intervals in brackets) controlled for repeated measures, breed, treatment, season, length of sow and all other factors listed in Table 4.1.

Table 4.5: Age effects on the time budgets of sows and gilts following the onset of parturition. Values are back-transformed REML estimates (95% confidence intervals in brackets) controlled for repeated measures, breed, treatment, season, length of sow and all other factors listed in Table 4.1. The regression estimate was from fitting age as a co-variate within parity. Within parities, differences between age group means ($p<0.05$) are denoted by different superscripts.

Behaviour	**Parity**	**Age of Sow (days)**					**Regression Estimate (x 10^{-4}) (+/- standard error)**
		256-355	**356-455**	**456-555**	**556-655**	**656+**	
Inactive (time spent)	1	54.9%^{a} (50.6 - 59.2%)	58.8%^{a} (56.2 - 61.4%)	87.9%^{b} (81.8 - 92.9%)	-	-	9.4 +/- 2.8
	2	-	-	57.8%^{a} (53.6 - 62.1%)	56.2%^{a} (53.6 - 58.9%)	54.7%^{a} (46.2 - 63.1%)	-3.8 +/- 3.2
Head-move (time spent)	1	38.7%^{a} (35.2 - 42.1%)	35.5%^{a} (33.4 - 37.6%)	9.4%^{b} (5.7 - 14.0%)	-	-	-8.8 +/- 2.3
	2	-	-	37.3%^{a} (33.9 - 40.8%)	38.0%^{a} (35.9 - 40.1%)	40.1%^{a} (33.3 - 47.1%)	3.8 +/- 2.6
Lateral lie (time spent)	1	85.7%^{a} (81.7 - 89.3%)	91.1%^{a} (89.1 - 92.9%)	96.3%^{a} (91.0 - 99.3%)	-	-	8.5 +/- 3.8
	2	-	-	93.3%^{a} (87.4 - 97.4%)	91.3%^{a} (82.8 - 97.1%)	91.8%^{a} (87.9 - 94.9%)	0.0 +/- 4.3
Look at piglets (time spent)	1	0.6%^{a} (0.4 - 0.8%)	0.6%^{a} (0.5 - 0.7%)	0.1%^{a} (0.0 - 0.4%)	-	-	1.2 +/- 0.8
	2	-	-	0.3%^{a} (0.2 - 0.5%)	0.5%^{a} (0.4 - 0.6%)	0.4%^{a} (0.1 - 0.8%)	0.6 +/- 0.9
Frequency of stepping (per 30 minutes)	1	1.7^{a} (1.5 - 2.0)	1.6^{a} (1.4 - 1.7)	1.1^{a} (0.8 - 1.4)	-	-	9.2 +/- 3.7
	2	-	-	1.4^{a} (1.2 - 1.5)	1.6^{a} (1.5 - 1.7)	1.5^{a} (1.1 - 1.9)	0.2 +/- 0.4

Breed Effects

Breed effects were partially confounded by breed differences in season of parturition, litter size and length of parturition (see Chapter 2). However, sufficient overlap existed between the breeds, in these measures, to separate these different factors influencing behaviour. In contrast, effects of sow genotype could not be separated from effects of litter genotype.

a) Sow Behaviour

Meishan-Landrace sows were found to be significantly less inactive than the other three breeds (see Table 4.3). Similarly, Meishan-Landrace sows spent significantly more time being in a general state of alertness ('head-move') than what Duroc or Landrace-Duroc sows did (see Table 4.1). These differences were most prominent at the start of parturition but there were no breed by time interactions.

Table 4.6: Percentage of the sample time spent in various behaviours and postures that differed between breeds (95% confidence interval in brackets). Values are back-transformed REML estimates controlled for repeated measures, breed, parity and treatment differences and all non-experimental factors listed in Table 4.1. Means with different superscripts were significantly different at $p<0.05$. See text for details.

Behaviour (time spent)	**Breed**			
	Duroc	**Landrace-Duroc**	**Meishan-Landrace**	**Meishan**
Inactive	63.2%^{a} (60.9 - 65.5%)	64.6%^{a} (60.5 - 68.5%)	50.2%^{b} (42.3 - 46.5%)	64.6%^{a} (60.6 - 68.6%)
Head-move	29.1%^{a} (26.9 - 31.3%)	28.2%^{a} (22.9 - 33.9%)	44.4%^{b} (42.3 - 46.5%)	32.9%^{ab} (27.2 - 38.8%)
Look at piglets	0.31%^{a} (0.23 - 0.41%)	0.50%^{ab} (0.34 - 0.69%)	0.70%^{b} (0.59 - 0.82%)	0.28%^{a} (0.16 - 0.42%)
Sit	0.08%^{a} (0.04 - 0.14%)	0.05%^{a} (0.00 - 0.14%)	0.80%^{b} (0.66 - 0.95%)	0.23%^{a} (0.10 - 0.40%)
Stand	1.06%^{a} (0.75 - 1.41%)	1.47%^{a} (0.89 - 2.19%)	0.91%^{ab} (0.66 - 1.19%)	0.14%^{b} (0.01 - 0.41%)
Ventral lie	3.22%^{a} (2.22 - 4.41%)	1.79%^{a} (0.65 - 3.48%)	5.04%^{ab} (3.91 - 6.31%)	8.77%^{b} (5.99 - 12.02%)

Meishan-Landrace sows and gilts spent more time looking at their piglets than Duroc sows and gilts or Meishan gilts (see Table 4.3).

There were no breed differences in the time the sows spent engaged in straw or floor-directed behaviour post-BFP or the frequencies of stepping and pushing back against the crate bars.

Breed differences were found for time spent sitting, standing and ventral lying but not for lateral lying (see Table 4.3).

b) Sow-piglet Interactions

Breed differences were found for frequencies of nose to nose and nose to body sow-piglet contacts, and also for frequency of not responding to piglets that approach the sows head (see Table 4.7).

Table 4.7: Breed differences in the frequency of nose to nose and nose to body sow-piglet interactions and in the frequency of not responding to piglets near the sows head per 30 minute sample (95% confidence intervals in brackets). Values are back-transformed REML estimates, controlled for repeated measures, season, parity, litter size, treatment and all factors listed in Table 4.1. Means with different superscripts differ significantly at $p<0.05$.

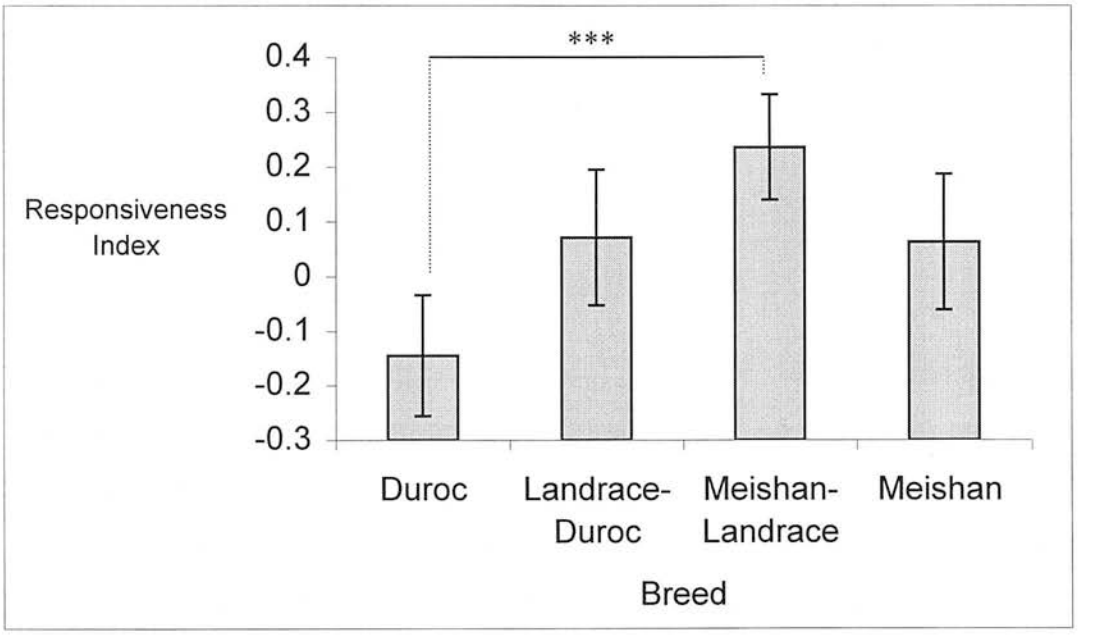
Behaviour (frequency per 30 minutes)	**Breed**			
	Duroc	**Landrace-Duroc**	**Meishan-Landrace**	**Meishan**
Nose-nose	1.57^{a} (1.48 - 1.67)	1.29^{a} (1.12 - 1.48)	2.10^{b} (1.99 - 2.21)	2.24^{b} (1.95 - 2.57)
Nose-body	2.10^{a} (1.97 - 2.25)	2.05^{ab} (1.84 - 2.27)	2.65^{b} (2.50 - 2.81)	2.34^{ab} (2.11 - 2.60)
No response	2.66^{ac} (2.48 - 2.86)	2.01^{b} (1.79 - 2.26)	2.30^{ab} (2.16 - 2.45)	3.14^{c} (2.79 - 3.53)

The breed differences for the frequency of nose to nose interactions was subject to a breed by parity interaction (Wald, $\chi^2 = 9.8$, d.f. = 2, $p<0.01$) and the differences shown in Table 4.7 were only present in parity one.

Meishan-Landrace sows and gilts made more nose to body contacts with their piglets than Duroc sows and gilts. There was also a tendency for Meishan-Landrace sows and gilts make more nose to body contacts than Landrace-Duroc sows and gilts ($t_{85} = 1.97$, $p<0.10$) (see Table 4.7).

The responsiveness index, which controlled for litter differences in the opportunity for sow-piglet interaction, also showed breed differences (see Figure 4.10). Meishan-Landrace sows and gilts were significantly more likely to respond to a piglet than Duroc sows and gilts (t_{124} = 4.28, $p<0.001$). Landrace-Duroc sows and gilts and Meishan gilts had intermediate responsiveness scores. There was no breed by parity interaction.

Figure 4.10: Breed differences in sows' responsiveness (+/- standard error) to piglets approaching her head, on the day of parturition (see methods for definition of responsiveness). The values presented are adjusted for repeated measures and controlled for parity, age of sow, season, litter size, time of day, farrowing house, whether straw was present, etc.



c) Sow Posture Changes

Breed differences were found for all posture changes except lie-stand, stand-kneel and kneel-lie. In most cases, where breed differences were found, Meishan-Landrace sows and gilts and Meishan gilts made more posture changes than Landrace-Duroc and Duroc sows (see Table 4.8).

Table 4.8: Frequencies of posture changes per hour found to differ between breeds (95% confidence intervals in brackets). Values are back-transformed REML estimates controlled for repeated measures, parity, treatment, litter size, season and all factors listed in Table 4.1. Means with different superscripts differed significantly at $p<0.05$.

Posture change (frequency per hour)	**Breed**			
	Duroc	**Landrace-Duroc**	**Meishan-Landrace**	**Meishan**
Flop (stand, sit or kneel to lateral lie)	1.87^{a} (1.80 - 1.94)	1.80^{a} (1.69 - 1.92)	2.19^{b} (2.12 - 2.26)	1.93^{a} (1.81 - 2.05)
Roll (ventral lie to lateral lie)	2.13^{a} (2.02 - 2.25)	1.81^{a} (1.64 - 1.99)	2.50^{b} (2.38 - 2.62)	3.02^{b} (2.74 - 3.33)
Lie-sit	3.42^{a} (3.21 - 3.65)	2.98^{a} (2.68 - 3.31)	4.58^{b} (4.33 - 4.85)	3.81^{ab} (3.44 - 4.23)
Sit-lie	2.00^{a} (1.88 - 2.13)	1.83^{a} (1.66 - 2.02)	2.86^{b} (2.70 - 3.02)	2.28^{ab} (2.07 - 2.52)
Lie - lie (changing lying postures, incl. roll)	3.16^{a} (2.93 - 3.40)	2.44^{a} (2.14 - 2.79)	3.96^{b} (3.71 - 4.22)	5.26^{c} (4.61 - 6.01)

Lying down to a lateral lying posture (flop) was more common amongst Meishan-Landrace sows and gilts than amongst Duroc ($t_{124} = 3.5$, $p<0.001$) and Landrace-Duroc sows ($t_{85} = 2.7$, $p<0.01$). Meishan, Landrace-Duroc and Duroc sows and gilts did not differ in their frequency of flopping. These breed effects were only found in the first few hours following BFP, resulting in a breed by time interaction (Wald, $\chi^2 = 33.9$, d.f. = 15, $p<0.01$).

Sitting up (lie-sit) was seen more often in Meishan-Landrace sows and gilts than in Duroc ($t_{124} = 3.3$, $p<0.01$) or Landrace-Duroc sows and gilts ($t_{85} = 3.8$, $p<0.001$). However this breed difference was only present during the first two hours following BFP, resulting in a breed by time interaction (Wald, $\chi^2 = 39.4$, d.f. = 15, $p<0.01$).

Once in a sitting posture a sow or gilt can either lie back down or stand up. There were no breed differences in the frequency of sit-stand posture changes. However,

Meishan-Landrace sows made more sit-lie posture changes than either Duroc (t_{124} = 4.0, $p<0.001$) or Landrace-Duroc sows (t_{85} = 4.0, $p<0.001$).

d) Piglet Location and Behaviour

Sow and gilt breed differences were also found in the proportion of their litters found in the creep, inactive at the udder and at the sows vulva, following the onset of parturition (see Table 4.9).

Table 4.9: Sow/gilt breed differences in the behaviour and location of their litters on the day of parturition. Values are percentages of a litter assigned to one of eight mutually exclusive piglet behaviour and location categories (see Chapter 2), calculated from successive five-minute scan samples of the litter. Values are back-transformed REML estimates controlled for repeated measures, parity, treatment, litter size, season and all factors listed in Table 4.1. Means with different superscripts were significantly different at $p<0.05$.

Piglet behaviour / location	**Breed**			
	Duroc	**Landrace-Duroc**	**Meishan-Landrace**	**Meishan**
Creep (per hour)	5.60^{a} (4.85 - 6.39)	2.10^{b} (1.33 – 3.04)	3.13^{b} (2.64 - 3.66)	2.00^{b} (1.25 - 2.93)
Udder inactive (per hour)	6.96^{a} (6.06 - 7.91)	11.31^{b} (9.76 – 12.96)	9.82^{b} (8.89 - 10.80)	13.27^{b} (11.60 - 15.03)
Sows' vulva (per 7 hours)	5.45^{a} (4.91 - 6.01)	2.47^{b} (1.96 – 3.03)	3.45^{b} (3.07 - 3.85)	3.52^{b} (2.91 - 4.18)

Breeds whose litters spent a lot of time inactive at the udder also spent less time in the creep, representing alternative strategies for keeping warm. Litters from with Duroc mothers spent more time in the creep and less time inactive at the udder than litters with mothers from the other three breeds.

Litters with Duroc mothers spent more time at the sows vulva than litters of either Landrace-Duroc ($t_{69} = 3.8$, $p<0.001$), Meishan-Landrace ($t_{124} = 3.0$, $p<0.01$) or pure-bred Meishan sows ($t_{70} = 2.3$, $p<0.05$).

Straw Effects

Straw was available to approximately half of the farrowing sows and gilts during the pre-farrowing period and during parturition. After parturition had finished, most of the straw was removed along with the placental membranes.

Table 4.10: The effect of the presence of straw in the farrowing crate on the behaviour of sows and gilts and the behaviour and location of their piglets on the day of parturition. The top three behaviours were measures taken on the sow or gilt. The bottom two behaviours are behaviour and location categories applied to the litters of sows. Values are back-transformed REML estimates controlled for repeated measures, breed and parity differences and all factors listed in Table 4.1.

Behaviour	**Treatment**		**Wald, χ^2, d.f. = 1, p-value**
	Straw	**No straw**	
Sitting (time spent)	0.14% (0.10 - 0.19%)	0.31% (0.24 - 0.38%)	p<0.05
Lie-stand (freq. per hour)	1.65 (1.61 - 1.69)	1.82 (1.78 - 1.86)	p<0.01
No response (freq. per 30 minutes)	2.29 (2.19 - 2.39)	2.71 (2.59 - 2.84)	p<0.02
Sows head (time spent)	1.41% (1.26 - 1.58%)	2.04% (1.85 - 2.24%)	p<0.02
Creep (time spent)	1.64% (1.35 - 1.95%)	4.93% (4.43 - 5.45%)	p<0.001

Straw had little effect on the behaviour of sows and gilts following the birth of the first piglet. The straw effects that were found are summarised in Table 4.10. Sows and gilts with access to straw spent less time sitting (Wald, $\chi^2 = 4.3$, d.f. = 1, $p<0.05$) and made fewer lie to stand posture changes (Wald, $\chi^2 = 9.6$, d.f. = 1, $p<0.01$) than sows and gilts without straw. In addition, when straw was present litters spent less time at the sow or gilt's head (Wald, $\chi^2 = 6.3$, d.f. = 1, $p<0.02$) and the sow or gilt made fewer no responses towards piglets (Wald, $\chi^2 = 6.4$, d.f. = 1, $p<0.02$) than when straw was absent.

There was also a strong effect of straw on the use of the creep by piglets. Piglets born into crates without straw spent more time in the creep than piglets in crates with straw (Wald, $\chi^2 = 37.7$, d.f. = 1, $p<0.001$).

There were no significant breed by straw interactions.

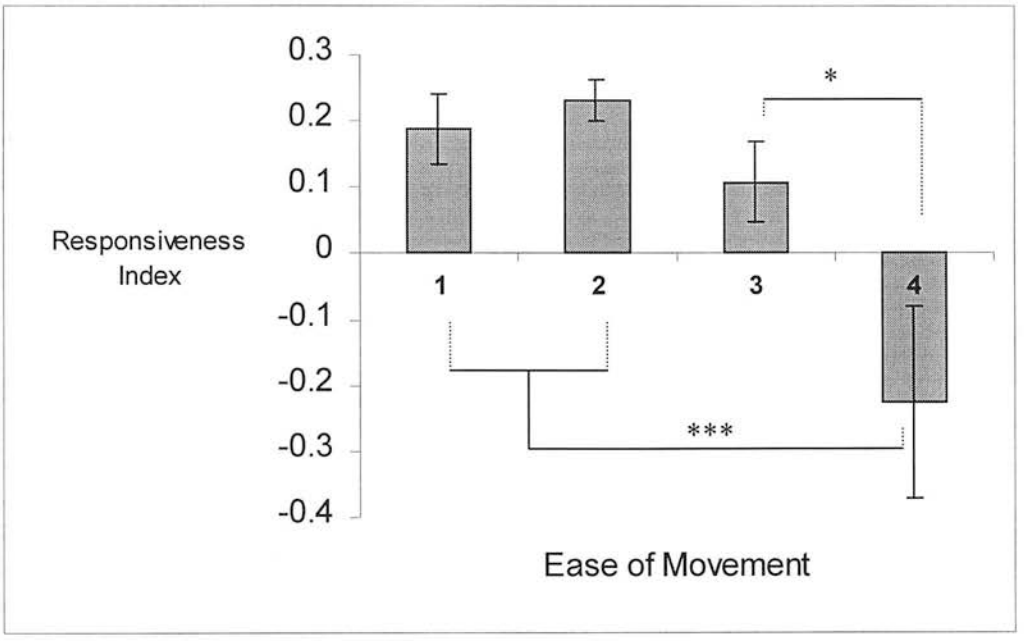
Other Effects

a) Ease of Movement Score

This was a subjective assessment of how well the sow moved from gestation pen to farrowing crate (see Chapter 2). The score was based whether the sow turned back against the person trying to move her, whether force had to be used to keep her moving in the right direction and whether the sow was aggressive. A high ease of movement score meant that the sow or gilt was difficult to move.

Ease of movement was found to be related to the sow or gilts responsiveness using the index described in the methods (see Figure 4.10). Only four sows or gilts were given an ease of movement score of four or five, so these were combined to form one category. Twenty-three sows and gilts scored three, 98 scored two and 34 scored one in the ease of movement assessment. Sows and gilts were difficult to move and had a score of four or five had a significantly lower responsiveness to piglets than sows and gilts that were easier to move and had a lower score (see Figure 4.10).

Figure 4.10: The effect of ease of movement (low score = moved easily) from the gestation pen to the farrowing crate prior to parturition on the responsiveness of sows and gilts to their piglets (+/- standard error). Values are back-transformed REML estimates controlled for repeated measures, breed, parity, treatment and all factors listed in Table 4.1.
* = p<0.05, *** = p<0.001



Analyses of the components of the responsiveness index, identified a low frequency of nose to nose contacts to be largely responsible for the low responsiveness of sows and gilts that were difficult to move (see Table 4.11). Ease of movement score did not influence the frequency of no responses or nose to body contacts.

Table 4.11: The effect of ease of movement score, measured during the move from gestation pen to farrowing crate, on the frequency of nose to nose sow-piglet contacts on the day of parturition. Values are back-transformed REML estimates controlled for repeated measures, breed, parity and treatment and all factors listed in Table 4.1 (95% confidence intervals in brackets). Means with different superscripts differ significantly at $p<0.05$.

Behaviour	**Ease of Movement Score**			
	1	**2**	**3**	**4**
Nose-nose (freq. per 30 minutes)	1.79^{ab} (1.70 - 1.89)	1.99^{a} (1.93 - 2.06)	2.07^{a} (1.95 - 2.19)	1.50^{b} (1.30 - 1.72)

b) Time of Day

Sows and gilts that started parturition between 01:01 and 07:00 hours, made significantly more flop posture changes than sows and gilts that began parturition at any other time of day (see Table 4.12). Starting parturition between 01:01 and 07:00 meant that at some point soon after parturition, sows and gilts would be given their daily ration of food.

Time of day also had an effect on the time sows spent sitting. Sows that started parturition between 19:01 and 01:00 hours spent less time sitting post-BFP than sows that began parturition at any other time of day (see Table 4.12).

Table 4.12: The effect of time of day when parturition starts on the subsequent behaviour of the sow or gilt. Values are back-transformed REML estimates controlled for repeated measures, breed, parity and treatment and all factors listed in Table 4.1 (95% confidence intervals in brackets). Means with different superscripts differ significantly at $p<0.05$.

Behaviour	**Time of Day (hours)**			
	07:01 - 13:00	**13:01 - 19:00**	**19:01 - 01:00**	**01:01 - 07:00**
Flop (freq. Per hour)	1.88^{a} (1.81 - 1.95)	1.96^{a} (1.91 - 2.01)	1.77^{a} (1.71 - 1.83)	2.18^{b} (2.09 - 2.27)
Sit (time spent)	$0.40\%^{a}$ (0.29 - 0.53%)	$0.20\%^{a}$ (0.14 – 0.27%)	$0.03\%^{b}$ (0.00 - 0.07%)	$0.37\%^{a}$ (0.24 - 0.52)

c) Farrowing House / Type of Crate

Type of farrowing house, old versus new, was associated with the type of farrowing crate found there (see Chapter 2). The effect of these differences in farrowing house or farrowing crate was reflected in the behaviour of the sow or gilt towards her piglets (see Table 4.13). This factor also influenced the frequency with which a sow or gilt pushed back against the back bar of the crate (see Table 4.13).

Table 4.13: Differences between the two types of farrowing house in the behaviour of the sow or gilt following the birth of the first piglet. Values are back-transformed REML estimates controlled for repeated measures, breed, parity and treatment and all factors listed in Table 4.1 (95% confidence intervals in brackets).

Behaviour	**Farrowing House**		**Wald, χ^2, d.f. = 1, p-value**
	Old	**New**	
Looking at piglets (time spent)	0.51% (0.42 - 0.60%)	0.22% (0.16 - 0.28%)	p<0.01
Nose-nose (freq. per 30 minutes)	1.87 (1.80 - 1.95)	1.61 (1.55 - 1.68)	p<0.02
Nose-body (freq. per 30 minutes)	2.49 (2.38 - 2.59)	2.08 (1.99 - 2.17)	p<0.01
Push back against bars (freq. per 7 hours)	2.03 (1.81 - 2.28)	1.08 (0.96 - 1.22)	p<0.001

d) Seasonal Effects

The practice of batch farrowing breeds (see Chapter 2) resulted in the effect of breed being partially confounded by season. Only two of the four breeds had sows and gilts farrowing in all four seasons, these were the Duroc and Meishan-Landrace. Meishan gilts were observed farrowing in two seasons, winter (December - February) and spring (March - April). Landrace-Duroc gilts were also seen farrowing in two seasons, spring and autumn (September - November), whilst Landrace-Duroc parity two sows were only observed farrowing in autumn. In the absence of parity effects, the spread of farrowings from the different breeds over the four seasons (see Chapter 2, Table 2.2) was sufficient to separate breed effects from season effects. REML frequently identified breed differences after controlling for season (see above), and identified season differences after controlling for breed.

Seasonal effects that persisted after controlling for all other influencing factors are summarised in Table 4.14.

Table 4.14: Seasonal differences in the behaviour of sows and gilts following the onset of parturition (95% confidence intervals in brackets). Values are back-transformed REML estimates controlled for repeated measures, breed, parity and treatment and all factors listed in Table 4.1. Means with different superscripts differed significantly at $p<0.05$.

Behaviour	**Season**			
	Dec – Feb	**Mar - May**	**Jun - Aug**	**Sep - Nov**
Sit (time spent)	$0.21\%^{a}$ (0.13 - 0.32%)	$0.71\%^{b}$ (0.59 - 0.83%)	$0.80\%^{b}$ (0.62 - 1.01%)	$0.63\%^{b}$ (0.50 - 0.79%)
No response (freq. per 30 minutes)	2.50^{ab} (2.33 - 2.68)	2.85^{a} (2.71 - 2.99)	2.39^{ab} (2.22 - 2.58)	2.20^{b} (2.07 - 2.34)
Sit-stand (freq. per hour)	1.13^{a} (1.07 - 1.20)	1.41^{b} (1.35 - 1.46)	1.39^{b} (1.31 - 1.48)	1.41^{b} (1.35 - 1.48)
Stand-kneel (freq. per hour)	1.17^{a} (1.10 – 1.24)	1.44^{b} (1.39 – 1.50)	1.42^{ab} (1.33 – 1.51)	1.46^{b} (1.39 – 1.53)
Lie-sit (freq. per hour)	1.43^{a} (1.32 – 1.56)	2.05^{b} (1.94 – 2.16)	1.88^{ab} (1.72 – 2.06)	1.79^{b} (1.68 – 1.92)
Sit-lie (freq. per hour)	1.36^{a} (1.26 – 1.46)	1.79^{b} (1.70 – 1.88)	1.68^{b} (1.56 – 1.82)	1.60^{ab} (1.51 – 1.70)
Kneel-lie (freq. per hour)	1.18^{a} (1.11 – 1.25)	1.46^{b} (1.40 – 1.52)	1.43^{b} (1.34 – 1.52)	1.46^{b} (1.40 – 1.54)
Flop (freq. per hour)	1.13^{a} (1.08 – 1.19)	1.37^{b} (1.33 – 1.42)	1.32^{b} (1.26 – 1.39)	1.32^{b} (1.27 – 1.37)
Percentage of the litter in the creep (per hour)	$3.56\%^{ab}$ (2.81 – 4.39%)	$4.94\%^{a}$ (4.32 – 5.60%)	$1.75\%^{b}$ (1.21 – 2.40%)	$2.76\%^{b}$ (2.19 – 3.39%)

Sows and gilts that farrowed in winter (Dec - Feb) spent less time sitting than sows and gilts that farrowed at any other time of year.

Sows and gilts that farrowed in winter made fewer posture changes associated with standing up and lying down (but not changing lying postures) than sows and gilts farrowing in Spring, Summer and Autumn (see Table 4.14).

Litters born in the summer used the creep much less on the day of parturition than litters born in the spring. Litters born in the autumn used the creep less on the day of parturition than litters born in spring (see Table 4.14).

Discussion

There were breed differences for the length of parturition, litter size and mean birth interval. In all cases, the difference was between Durocs and the other three breeds. Durocs are the only breed represented in the current study whose dam line has not been subject to artificial selection for litter size (see Chapter 2). Thus, selection for litter size appears to have resulted in shorter parturitions and shorter birth intervals. Long birth intervals and long parturitions tend to be associated with the occurrence of stillbirths or low viability piglets (Randall, 1971; Fraser *et al.*, 1997). Consistent with this association, the litters of Duroc sows and gilts spent more time at the sows vulva than the litters from other breeds.

A previously unreported consistency in the expression of sow-piglet interactions over parities one and two was found in this study. Nose to nose and nose to body contacts, pushing piglets away with the snout and not responding to piglets all showed consistency of expression within individuals over parities one and two. Consequently, responsiveness to piglets was also consistent within sows over the first two parities. These findings suggest stable maternal types of sow that differ in how they respond to piglets. All of these measures of sow-piglet interactions showed significant breed differences. Consistency of expression over time and the presence of breed differences suggest that the responsiveness of sows to their piglets is subject to genetic influences. Nose to nose interaction with piglets is thought to be the behavioural mechanism by which mother-offspring bonds develop (Grundlach, 1968; Whatson and Bertram, 1983; Jensen and Redbo, 1987). Based on the data presented here, it would appear that the importance sows place on bonding with piglets on the day of parturition is partly explained by genotypic differences.

Variation between sows and gilts in their responsiveness to piglets was linked to how easily sows and gilts could be moved from the gestation pen to the farrowing crate, previously unreported in the literature (c.f. Ahlstrom, 1997). Thus sows and gilts that were difficult to move were much less responsive to their piglets, making fewer nose to nose contacts, than sows and gilts that could be moved easily. Therefore, an ease of movement score from gestation pen to farrowing crate would appear to have some

potential for predicting the maternal style of the sow or gilt. In later Chapters I will explore whether sow responsiveness towards piglets has any functional consequences for piglet survival.

Changes over the course of parturition and immediately after parturition show a gradual decrease in sows responsiveness to piglets. This was due to an increase in not responding to piglets over time. The frequency of nose to nose and nose to body contacts between sows and piglets did not vary over time during the day of parturition. These changes in how a sow or gilt interacts with her piglets have not previously been reported in the literature.

Differences between the breeds in the time spent looking at piglets and interacting with piglets suggest that Landrace genes are associated with an increased awareness of their piglets. The presence of Meishan genes may interact with the Landrace genes to further increase sow responsiveness to piglets. Furthermore, since there were no breed differences in the proportion of time a litter spends near the sows head, these breed differences would appear to be largely due to maternal factors rather than litter factors. Breed differences in the responsiveness of sows towards their piglets have not previously been reported but these differences may underlie breed differences in piglet rearing ability.

The frequency with which sows and gilts stood up and laid down was consistent within individuals over parities one and two. Laying down posture changes have previously been associated with a high risk of piglet crushing (Edwards *et al.*, 1986; Olsson and Svendsen, 1989; Weary *et al.*, 1996a). Therefore, a sow's risk of crushing may also be consistent over the first two parities (this will be explored more fully in later Chapters). This supports the findings of Wechsler and Hegglin (1997) who showed that posture changing behaviour in the current parity could predict a sows incidence of crushing in previous parities. Many types of posture change did show breed differences in their frequency of expression. However the frequency with which sows and gilts stood up from sitting and laid back down again did not show breed differences. This suggests that the risk of crushing cannot simply be reduced by creating new synthetic breeds with different component pure-breds. If risk of crushing

were heritable, which the consistency in the frequency of lying down found here supports, artificial selection would need to take place within genotypes.

The breed differences found for frequency of posture changing all pointed to the Meishan-Landrace and the Meishan pure being more restless than the Duroc and Landrace-Duroc. This finding is either inconsistent with the idea that Meishan genes are linked to good maternal behaviour or that lying still following the onset of parturition is not necessarily a good maternal trait. However, for some types of posture change (e.g. flop) Meishan-Landrace sows and gilts made significantly more posture changes than Meishan gilts. This indicates that the propensity to perform these types of posture change may not be an effect of Meishan genes. In contrast, changing lying postures was seen more frequently in Meishan pure than Meishan-Landrace, which in turn performed more than Landrace-Duroc and Duroc pure breeds. Time spent in a ventral lying posture showed similar breed differences. Thus changing lying postures frequently and lying ventrally may be associated with Meishan genes. Changing lying postures is thought to be one of the posture changes that result in the crushing of piglets (Weary *et al.*, 1996a; Wechsler and Hegglin, 1997). The role of different posture changes in the crushing of piglets, and whether these breed differences in posture changing behaviour results in breed differences in the incidence of crushing will be explored more fully in later Chapter.

Meishan-Landrace sows and gilts do more lie to sit posture changes than Landrace-Duroc and Duroc sows and gilts but these three breeds do equivalent amounts of sit to stand posture changes. This results in Meishan-Landrace sows and gilts spending more time sitting than the other three breeds. Sitting is thought to be an abnormal posture in pigs associated with restrictive environments (Lembeck *et al.*, 1996), as a response the frustration of feeding motivation (Lewis, 1999) and in reaction to inescapable electric shock (Jensen *et al.*, 1996). Thus, the behaviour of Meishan-Landrace sows and gilts suggests that this breed is the least well adapted to the farrowing crate. This is an unusual result since the Meishan-Landrace has been the subject of artificial selection for litter size in the farrowing crate (Dr. A. D. Hall, pers. comm.). A degree of adaptation to the farrowing crate, concurrent with artificial selection for litter size, might have been expected, however it would seem from these results that this has not happened. It is interesting to note that the Meishan pure did

not spend more time in the sit posture than the Landrace-Duroc and the Duroc breeds. However, this may be more a consequence of poor leg strength in the Meishan (White *et al.*, 1995) than better adaptation to the farrowing crate. In contrast, Duroc and Landrace-Duroc breeds are known to have larger leg muscles than the Meishan breed (Young, 1992), so Duroc and Landrace-Duroc sows and gilts would have been easily capable of sitting up frequently.

Consistency within individual sows over parities one and two was also found for the behaviour of their litters. In particular, the proportion of the litter found inactive away from the creep or the sow or present at the sows vulva. These measures of piglet behaviour and location are likely to be higher amongst weak, low viability litters. Therefore, this result indicates that the propensity of a sow to have weak, low viability litters is consistent over parities one and two. This result when linked with the previously mentioned breed difference for the proportion of a litter found at the sows vulva, suggests that the propensity of a sow to produce low viability piglets may have a genetic basis. However, this finding is not consistent with the work of Siewerdt and Cardellino (1998) who found that the number of stillbirths is a sow trait that has only low repeatability.

Time spent active at the udder was lower between nine and twenty-four hours following the onset of parturition (BFP) than during the six hours following BFP. This would seem to reflect the development of a suckling rhythm developing in conjunction with patterns of milk letdowns (Lewis and Hurnik, 1985; de Passille *et al.*, 1988; de Passille and Rushen, 1989). In addition, the use of the creep was much higher, and time spent active away from the sow or creep was lower, between nine and twenty-four hours post-BFP than during the six hours following BFP. Thus, regular patterns develop in the behaviour of piglets during the first day of life. During the first few hours of life, piglets can be found in all areas of the crate but towards the end of the day piglets tend to be either suckling at the udder or in the creep. This is consistent with the development of behavioural synchrony amongst litters described by de Passille and Rushen (1989).

Time spent inactive at the udder increased from the onset of parturition until six hours post-BFP and was subject to breed differences. The litters of Meishan-Landrace,

Meishan pure and Landrace-Duroc sows and gilts spent more time inactive at the udder than the litters of Duroc sows and gilts. Litters appeared to spend more time inactive at the udder in exchange for spending less time in the creep, representing alternative strategies for keeping warm. Resting at the udder is a trait associated more with Meishan piglets than Large White piglets (Meunier-Salaun *et al.*, 1991). However, the results from this study would suggest that this behaviour is not just a trait of Meishan piglets since the piglets of Landrace-Duroc sows and gilts spend similar amounts of time inactive at the udder. Lying inactive at the udder may be sensitive litter size, since Meishan gilts lad very large litters that were only marginally larger than those of Landrace-Duroc sows and gilts. The usefulness of resting at the udder for thermoregulatory purposes is likely to increase with the number of piglets huddling together at the udder.

This study found no breed by treatment interactions or breed by farrowing house interactions, indicating that behavioural breed differences were not dependent on the differences between farrowing crates and the presence of straw. Sows and gilts in crates with straw spent less time sitting and made fewer lie to stand posture changes than sows and gilts in crates without straw. As already mentioned, the sit posture is thought to be an indicator of restriction, frustration or stress, therefore the presence of straw would seem to reduce the aversive effects of being in a crate. This is perhaps achieved through the increase in comfort associated with having straw to lie on.

The presence of straw in the farrowing crate was strongly associated with reduced use of the creep by litters compared to when straw was absent. This is similar to what Cronin and Smith (1992) found when they compared straw-bedded pens with farrowings crates without straw. In the Cronin and Smith (1992) study, effects of straw cannot be separated from effects of restriction. However, a more recent study compared crates without straw with pens without straw and similarly found that piglets in crates rest underneath the heat lamp more than piglets in pens (Blackshaw *et al.*, 1994). Thus, the use of the creep or heat lamp depends on both the presence of straw and the accessibility to the sows udder. The reduced use of the creep when straw was available may have resulted in more piglets being at risk of crushing. This potential effect of straw will be explored in Chapter 5.

A consequence of litters without straw using the creep more was that piglets would need to pass the sows head more frequently on route to the creep. This resulted in a higher frequency of not responding to piglets but no effect on the overall responsiveness of sows towards their piglets. This is in contrast to what Herskin *et al.* (1998) found when they measured sow responsiveness to a piglet squeal, in an open farrowing system, with or without nesting materials.

There were few behavioural differences between parity one gilts and parity two sows, which supports the findings of others (Hutson *et al.*, 1992; Bøe, 1994). Parity two sows spent less time lying ventrally and changed lying postures less frequently than parity one gilts. This indicates that parity one gilts are more restless than parity two sows and may be linked to the smaller pre-farrowing cortisol response in parity two sows compared to parity one gilts in crates (Jarvis *et al.*, 2001, in press).

Age was found to co-vary with many behaviours observed in parity one gilts but not for many behaviours seen in parity two sows. Young gilts were more active and stepped more than older gilts, whilst spending more time looking at piglets and rooting piglets away. This suggests that young gilts are more nervous of their piglets or the situation they find themselves than older gilts. This finding may explain why young gilts have reduced productivity in parity one compared to older gilts (Legault *et al.*, 1996; Cozler *et al.*, 1998). Since age was almost completely confounded by parity, it is impossible to say whether maturity interacted with experience.

Summary and Conclusions

This study has identified several important characteristics of sow maternal behaviour. Several aspects of the sows behaviour indicate the existence of stable maternal types between parities one and two. Most notably, these behaviours were the propensity of a sow to interact with her piglets and the frequency with which a sow stood up and laid back down again on the day of parturition. Differences between sows in relation to these behaviours are likely to have functional consequences in terms of piglet survival and mortality. This idea will be developed more fully in later Chapters. In addition, sows appeared to be consistent in their tendency to produce litters with reduced viability (as measured by the activity and location of the litter). Breed differences were identified for the propensity of a sow to interact with her piglets, indicating that this aspect of maternal behaviour can be modified through the development of new synthetic lines. In contrast, no breed differences were found for the frequency of standing up and lying back down again, which are likely to be linked to a sows risk of crushing (see later Chapters). Therefore, the development of commercial breeds that make fewer of these posture changes would need to select within breeds.

CHAPTER 5:

NON-BEHAVIOURAL LITTER FACTORS LINKED TO THE INCIDENCE OF PIGLET PRE-WEANING MORTALITY

Introduction

If gestation has gone well then the majority of the foetuses implanted in the sow uterus approximately 112 days before will have developed through to term. The neonatal (pre-parturient) piglet is then faced with a set of whole new challenges, the first of these being the birth process.

For any young mammal, the transfer from the warm, protective, nutrient-providing uterus to the cooler, more variable and dangerous outside world represents perhaps the biggest physiological challenge of it's life. Surviving the birth process and becoming established independent of the umbilical cord requires the piglet to breath for itself, maintain its own body temperature and obtain food by finding and successfully competing for a teat.

The piglet's chances of surviving the birth process are influenced by piglet viability at term and the ease with which the sow expels her piglets. Long birth intervals tend to be associated with the birth of still-born piglets (English, 1969; Randall, 1972; Fraser *et al.*, 1997) or piglets whose viability may be seriously impaired by being starved of oxygen (English and Morrison, 1983). Piglet viability at term will influence: a) the ability of the piglet to survive being temporarily without oxygen during constriction of the umbilical cord, and b) the ability of the piglet to aid its own delivery. Viability at birth is therefore a consequence of the interaction between viability at term and the ease of expulsion. Viability at birth effects the ability of the piglet to maintain its body temperature outside the uterus and to compete for food (English and Smith, 1975; Thompson and Fraser, 1986).

The normal deep body temperature of the piglet is 39°C (English and Morrison, 1983) and the lower critical body temperature of singly-housed piglets is 34°C (Mount, 1968), below this temperature the piglet must raise its metabolism, utilising its glycogen reserves for heat production. Heat retention is aided by piloerection, surface vasoconstriction and having an insulating fat layer. Piloerection is likely to be of limited use for the virtually hairless commercial genotypes of pig. Insulation from a fat layer is also of limited use since body fat generally constitutes only 1-2% of body composition in new-born piglets (English and Morrison, 1983). Environmental factors such as the presence of a heat lamp and straw in the farrowing pen, as well as behavioural strategies such as piglets huddling together and sharing body heat with the sow, can help prevent piglets from getting too cold and improve survival (Christison *et al.*, 1997). At sub-optimal temperatures, the piglet reduces its locomotor vigour (Stephens, 1971) making it less able to compete for a teat and more prone to crushing (Curtis, 1974).

After surviving the birth process the initial problems of breathing and thermoregulating, the next big challenge facing the new-born piglet is finding food. It is essential that piglets receive nutrition as soon as possible following birth since they are born with only low energy reserves, which are depleted rapidly when they have to be used to maintain body temperature (English and Morrison, 1983). Studies show that piglets that miss the first few nursings can be at a severe disadvantage to their siblings (Thompson and Fraser, 1988). However, simply locating a teat is not the only problem the piglet faces when trying to obtain its mothers milk, it must also compete with its litter mates. Piglets are born with sharp teeth perfectly adapted to the type of sideways biting movements seen during teat disputes (Fraser, 1975; Fraser and Thompson, 1991). Piglets born towards the end of parturition tend to be smaller and less viable than those born earlier (English *et al.*, 1982; English and Wilkinson, 1982), yet they are further disadvantaged by there being less space at the udder for them. With continuing selection for litter size, space at the udder will be further reduced such that piglets born towards the end of parturition may not be able to find a free teat. Competition between piglets for teats and space at the udder has been identified

as a mechanism through which facultative siblicide can act (Fraser, 1990; Fraser *et al.*, 1995).

Facultative siblicide is an adaptive mechanism whereby siblings compete for a common resource (e.g. food from the mother), which ensures that when the resource becomes limited the fitter sibling survives at the expense of the less fit sibling (Mock, 1984). Facultative siblicide suggests that sibling competition, and mechanisms that promote sibling competition, are adaptive (Fraser, 1990; Fraser *et al.*, 1995). Pigs fit the pattern for facultative siblicide (Mock, 1984), having small extra investment to produce spare young, sibling competition and weaponry, and a competitive asymmetry between litter mates (Fraser, 1990; Fraser *et al.*, 1995). Competitive asymmetry between litters mates, in weight and viability, is found in Wild boar (Fernandez-Llario *et al.*, 1999) as well as domestic pigs (Thompson and Fraser, 1988), suggesting mechanisms that promote facultative siblicide have evolved in this species.

Over the first week after birth, piglets develop teat fidelity (de Passille *et al.*, 1988). Piglets that continue to compete and fight for teats often end up missing milk ejections resulting in reduced weight gain (de Passille *et al.*, 1988). Weary *et al.* (1996b) showed that piglets that have poor weight gain are more likely to be crushed because they remain close to the sow between milk ejections. Sibling competition can therefore affect piglet survivorship. In situations where the sow has a poor milk supply, the degree of competition between siblings is higher and piglets continue to fight over teat access for longer (de Passille and Rushen, 1989). These results suggest that crushing and starvation are different end-points to the same process of sibling competition (Fraser, 1995).

A distinction should be drawn between mortality risk factors that influence individual piglets (e.g. birth weight and viability) with risk factors that affect the entire litter (e.g. maternal quality of the sow). Several studies have published data suggesting that some litters are more prone to piglet mortality than others (Bel Isle and England, 1978; Maddock, 1980; Dyck and Swierstra, 1987; Fraser *et al.*, 1988; de Passille and Rushen, 1989). These studies have highlighted the importance of identifying litter risk factors related to piglet mortality. One way of moving towards identifying potential

causal risk factors is to compare the characteristics of high and low mortality litters. A factor often quoted as co-varying positively with the incidence of piglet mortality is litter size (Fahmy and Bernard, 1971; Sadana and Singh, 1972; Nielsen *et al.,* 1974; Bille *et al.*, 1974; Edwards *et al.*, 1986, 1994; de Passille and Rushen, 1989). Another factor that has sometimes been found to co-vary positively with piglet mortality is the degree of birth weight heterogeneity (English and Smith, 1975; Daza *et al.*, 1999; but see van der Lende and de Jager, 1991; Lee and Haley, 1995 for conflicting results). Both of these factors fit with the hypothesis that sibling competition is an important mediator of piglet mortality (English and Smith, 1975; Fraser, 1990; Fraser *et al.*, 1995). De Passille and Rushen (1989) found that the biggest factor predicting piglet mortality was initial poor weight gain suggesting that some sows are not producing sufficient milk or colostrum immediately after parturition.

Changes to farm management practices, such as careful tooth clipping not down to the gum line can reduce piglet mortality (Palechek and McIntosh, 1993) and improve weight gains (Weary and Fraser, 1999). The practice of cross-fostering in order to minimise the weight variation within a litter can also reduce the mortality rate (English *et al.,* 1977; Marcatti Neto, 1986) but this must be done within the first two days following farrowing (Straw *et al.*, 1998).

Other factors often quoted as influencing piglet mortality are time of the year (Gracey, 1955; Pomeroy, 1960; Sadana and Singh, 1972; Nielsen *et al.*, 1974; Vrbanac *et al.*, 1995), whether farm staff are available to assist with farrowing (Dyck and Swierstra, 1987) and the behaviour of the sow (Fraser, 1990; Marchant *et al.*, 1996; Wechsler and Hegglin, 1997).

Later Chapters will look at how sow behaviour can influence piglet mortality, but the current Chapter will describe some of the non-behavioural factors influencing piglet mortality. These factors include various measured environmental differences between the litters studied that were not under experimental control (e.g. season, age of sow, litter size, length of parturition). Other non-behavioural factors include those built in to the experimental design, these were breed, parity and the presence of straw in the farrowing crate.

Methods

Data relating to cause and timing of each pre-weaning mortality from 210 sow litters was collected over 25 months from March 1998 until April 2000. There were 142 parity one gilts and 68 parity two sows, with the 68 of these sows being monitored in their second parity. The cause of each pre-weaning piglet mortality was the opinion of the farm staff taking care of the farrowing sow and they used the definitions shown in Table 5.1. However, video verification of the cause of each mortality could be made for 159 of the 210 sow litters studied here (see Chapter 2, p. 29). In practice, this video verification accounted for all still-births, most savagings and many of the crushing mortalities that occurred in these 159 sow litters.

Table 5.1: The causes of mortality and how they were defined

Cause of Death	Operational definition
Still-birth	Fully developed piglets born dead or dying within the first few minutes following birth. Intra-partum still-births were not distinguished from gestational still-births.
Crushed	Piglets found dead showing signs of being laid on by the sow; e.g. squashed rib cage, red spots on the nose indicating blood having been forced towards the head.
Savaged	Piglets found dead with large bite marks associated with the sows mouth size and not from sibling fights.
Starved	Piglets found dead after several days of noticing that the same piglet was failing to compete successfully for a teat. Small piglets with poor weight gain.
Congenital Abnormality	Piglets born with genetic defects which seriously reduced their chance of survival. Examples include, splayed legs, heart problems, blind anus, joint illness. These piglets either die naturally or are culled.
Non-viable	Small, weak piglets unlikely to survive. Most of these are culled before they would succumb naturally.
Other (unknown or unspecified)	This category is reserved for deaths where the cause is either unknown or unspecified.

Statistical Analysis

Exploratory analysis

To help understand the nature of the mortality data set, I undertook an exploratory analysis of the data. The relative contribution of each identified 'cause' (as defined by Table 5.1) to the total incidence of piglet mortality was calculated. To explore whether the distribution of mortalities between litters occurred randomly, the

distribution of mortalities was tested for goodness of fit to a Poisson distribution using the Chi-squared test. Genstat (Version 5, Release 4.1, 1998, Lawes Agricultural Trust) was used throughout for all statistical analyses.

Information regarding the occurrence of savaging, crushing and starvation mortalities during the lactation period is presented as a Table.

Cross-fostering was used to balance out litter size between sows. Therefore, litters with many still-births could also be subject to pre-weaning mortalities such as crushing because piglets were fostered on to these sows. This made it possible to explore relationships between the occurrence of the different types of mortality identified in Table 5.1 using Chi-squared two by two contingency Tables (see below for an example).

		Crushing	
		Yes	No
Starvation	Yes		
	No		

Confirmatory analysis

Generalised Linear Models, fitting a binomial distribution and using a logit link function, were used to model the incidence of still-births and the incidence of crushed piglets. The number of still-births per litter was modelled using a binomial total of three, whereby litters with three or more still-births were grouped into one category. The number of crushed piglets per litter was modelled using a binomial total of two, whereby litters with two or more crushed piglets were grouped into one category. Terms were objectively fitted to each model in turn using Stepwise Regression. The first term fitted was the one that reduced the residual mean deviance the most. When residual mean deviance approaches a value of 1, all sample variation is explained by the model. Terms were then either added or dropped from the model depended upon what action minimised the residual mean deviance.

The model produced by the Stepwise Regression procedure was then used in a Generalised Linear Mixed Model (GLMM) Analysis, which fitted a random model in addition to the fixed model. The Random model described the structure of the data, i.e. sow nested within parity (sow/parity). As before, a binomial distribution was fitted with a logit link function. The random model split the residual variance into two strata - the sow stratum and the sow.parity stratum. In instances where the variance component for the sow stratum was zero, all variability could be explained at the within sow level and not between sow level. When this happened the model of choice was the Generalised Linear Model, and estimates for the model terms were taken from the original Generalised Linear Model. When the residual variance component for the sow stratum of the random model was greater than zero, estimates for the model terms were taken from the GLMM.

The final model included fixed effects of breed, parity, treatment, season, farrowing house and information relating to cross-fostering practices. The model also included the covariates of age of sow, litter size and length of parturition.

The effects of individual model terms are described in two ways: a) the effect of adding the term to the model, in the order specified, on the deviance of the model (i.e. how well it fitted the data); b) estimates of individual parameters of the model were calculated taking into account all the other terms in the model. The first technique is often referred to as the 'model-driven approach', whereas the second technique is a 'data-driven approach' and is the more conservative of the two.

Cross-fostering occurred frequently but the number cross-fostered and whether piglets were fostered onto a sow or off of a sow varied between litters. In an attempt to account for these differences between litters, cross-fostering was fitted as a factor with the following levels:

1. No cross-fostering occurred (n = 106)
2. Two or fewer piglets were fostered off (n = 24)
3. Two or fewer piglets were fostered on (n = 28)
4. Three or more piglets were fostered off (n = 23)
5. Three or more piglets were fostered on (n = 28)

Time of year when the sow farrowed was divided up into the four Northern hemisphere seasons, as follows. The temperature within the farrowing houses was also monitored and means were calculated for each season.

1. Winter: December - February (n = 37)
2. Spring: March - May (n = 93)
3. Summer: June - August (n = 32)
4. Autumn: September - October (n = 48)

Breed differences were confounded by litter size, length of parturition and season but enough overlap existed between the breeds to allow the modelling process to identify the relative contributions of these factors and covariates to the mortality statistics.

Many of the breeds studied were "batch farrowed", i.e. sows and gilts of the same breed were serviced at about the same time so that they would farrow at the same time of year. However, two breeds were observed farrowing over all four seasons and two breeds were observed farrowing over two seasons (see Table 5.2).

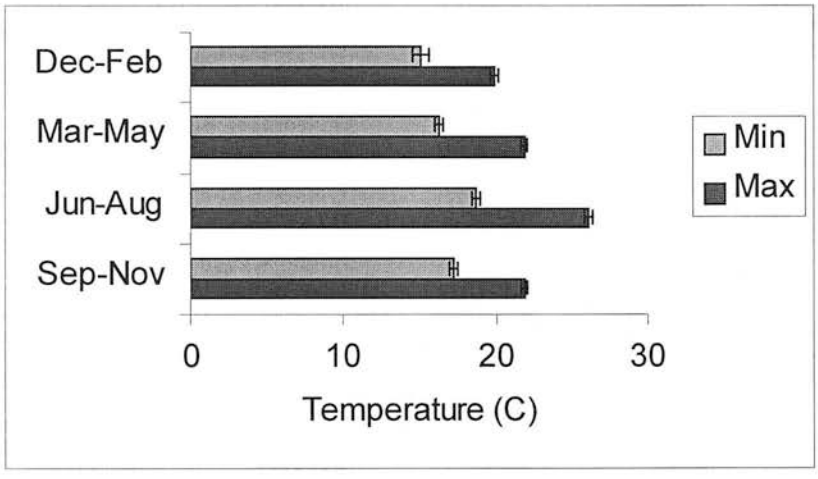
Table 5.2: The distribution of farrowings from each breed over the four seasons.

	Winter	**Spring**	**Summer**	**Autumn**
Duroc	8	45	5	23
Landrace-Duroc	0	11	0	8
Meishan-Landrace	23	23	27	17
Meishan	6	14	0	0

Farrowing House Temperature

All farrowing houses were fitted with extractor fans that were controlled via thermostat and creep lamps provided all the heating (sows and piglets also contributed to the heating). These devices reduced the variation in temperatures over the year but there was still some seasonal variation in temperature within the farrowing house (see Figure 5.1).

Figure 5.1: Mean minimum and maximum temperatures (+/- standard error bars) in the farrowing houses over the four seasons.

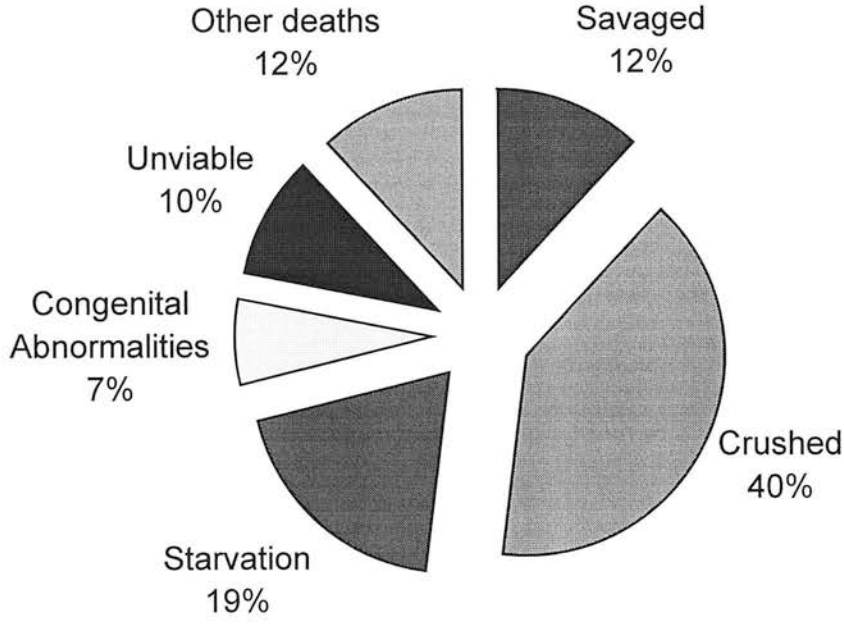


The differences between the minimum and maximum temperature reflects the daily range in temperature within the farrowing house. There was considerable overlap between the seasons in the daily range of temperatures experienced in the farrowing house. However, the standard error bars show that the minimum-maximum temperatures during Summer (June - August) are higher than at other times of year. In addition, the maximum temperature reached in Winter (December - February) was lower than at other times of year.

Causes of Mortality

Mortality information was collected from 210 litters - 142 gilt litters and 68 of these were also recorded in their second parity. A total of 2139 piglets were born alive from these sows, whilst 146 still-births and 98 mummies (pre-term foetuses) were expelled along with these live piglets. This equates to 4.1% of developing foetuses dying prior to reaching term, and a further 6.4% of piglets that developed to term, being born dead. Of the 2139 piglets that survived parturition, a further 7.2% (154) died prior to weaning: 64 were crushed by the gilt/sow, 31 were found starved to death and 20 were savaged by the gilt/sow. In addition, there were 12 congenital abnormalities resulting in death and 14 piglets culled after being deemed to be non-viable. In 20 cases, the cause of death was unknown or not recorded ('other'). The causes of these pre-weaning mortalities, as defined in Table 5.1 are displayed in Figure 5.2.

Figure 5.2: Causes of pre-weaning mortality amongst live-born piglets (as defined in table 5.1

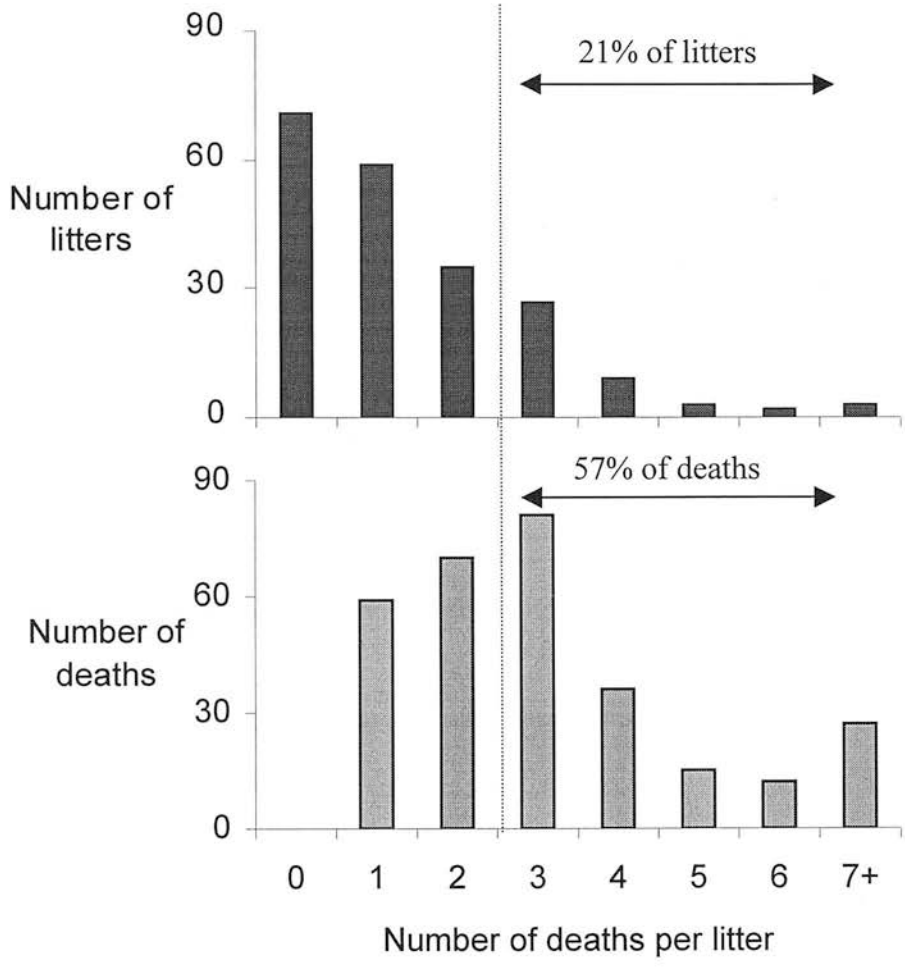


The Spread of Piglet Mortality Over the Population of Sows

Sows and gilts with three or more piglet mortalities (21.1% of litters) accounted for 57.0% of all piglet mortalities (including still-births, see Figure 5.3), whilst 12.8% of gilt/sow litters accounted for 50.3% of all the pre-weaning mortalities (not including still-births).

The overall mortality data (including still-births, top graph, Figure 5.2) was compared to the frequencies predicted by the Poisson distribution (after Fraser, 1990). The Poisson distribution assumes a random distribution of counts. The distribution of total mortality amongst the litters was found to deviate significantly away from what would be expected if the occurrence of mortality was random ($\chi^2 = 18.47$, d.f. = 4, $p<0.001$). Pre-weaning mortality (not including still-births) was an even poorer fit to the Poisson distribution ($\chi^2 = 20.67$, d.f. = 3, $p<0.001$). In both cases, there were more litters than expected with zero mortalities and more litters than expected with many mortalities (4 or more for total mortality, 3 or more for pre-weaning mortality).

Figure 5.3: Frequency distributions showing the number of litters with different numbers of piglet deaths (top graph) and how the relatively few litters can account for the majority of the total piglet mortality (bottom graph - 300 mortalities) (based on an idea for graphing from Varley, 1995).



Timescale for the Occurrence of Pre-weaning Mortalities

Of the six causes of mortality shown in Figure 5.2, savaging, crushing and starvation are likely to be most influenced be the maternal behaviour of the sow. Piglets born with congenital abnormalities or deemed to be non-viable by farm staff were often culled before they would otherwise die naturally. Mortalities assigned to the 'other' category were those whose cause either went unrecorded, or situations where the cause of death was unknown. For these reasons only the time-scales for deaths through starvation, savaging and crushing are presented in Table 5.3.

The majority of the savaging deaths occurred during the first day following parturition, savaging did not occur after the third day following parturition. The majority of crushing deaths occurred over the first four days following parturition, although crushing also occurred in the second and third weeks post-partum. Deaths through starvation were only found after the day of parturition. Piglets died by starvation throughout the suckling period, even in the week before weaning, but the majority died during the first week (see Table 5.3).

Table 5.3: The distribution of savaging, crushing and starvation mortalities over the lactation period. Day 0 = day of parturition.

Mortality	**Day**								**Week**	
type	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**2**	**3**
Savaging	13	4	0	1	0	0	0	0	0	0
Crushing	15	18	11	5	3	0	0	0	8	1
Starvation	0	2	4	4	3	3	5	0	7	1

Relationships Between the Different Causes of Mortality

The occurrence of one type of mortality did not significantly influence the occurrence of another type of mortality (see Table 5.4). On the basis of this result, the different types of mortality were analysed separately in the confirmatory analysis.

Table 5.4: Chi-squared values (d.f. = 1) for pair-wise comparisons for the presence or absence in a litter of the seven types of piglet mortality defined in Table 5.1. Critical value of Chi-squared at one degree of freedom = 3.84. A high value of Chi-squared indicates that the occurrence of one mortality type in a litter was positively influenced by the occurrence of the other mortality type in a pair-wise comparison.

Crushings	0.34					
Savagings	0.48	0.64				
Starvations	0.19	**3.19**	0.16			
Cong. abnorm.	0.01	0.36	0.77	0.02		
Non-viable	2.58	1.01	**3.35**	1.01	**3.35**	
Other	0.11	0.07	0.01	0.95	0.01	1.15
	Still-births	Crushings	Savagings	Starvations	Cong. abnorm.	Non-viable

There were tendencies ($p<0.10$) for: a) starvation mortalities to be more common in litters that also had crushing mortalities (8/50) than in litters without (12/160), b) non-viable piglets to be more common in litters with savagings (2/12) than without (9/198), and c) non-viable piglets to be more common in litters with congenital abnormalities (2/12) than without (9/198).

Breed Differences in Litter Size, Sow size and Length of Parturition

There were breed differences in the mean litter size and mean length of parturition (see Chapter 4), but there was also considerable overlap between the breeds as Tables 5.5 and 5.6 show. In addition, the apparent length of the sow, as measured from video, also showed considerable overlap between the breeds (see Table 5.7).

Table 5.5: Breed variation in litter size.

Breed	Litter Size		
	Minimum	Median	Maximum
Duroc	3	10	16
Landrace-Duroc	5	11	14
Meishan-Landrace	4	11	17
Meishan	3	12	16

Table 5.5: Breed variation in parturition length (measured to the nearest five minutes). Sows with parturitions that exceeded the six hour observation period were given the same parturition length of 360 minutes.

Breed	Parturition Length (minutes)		
	Minimum	Median	Maximum
Duroc	105	262.5	360
Landrace-Duroc	70	135	360
Meishan-Landrace	25	210	360
Meishan	70	140	360

Table 5.7: Breed variation in sow length, as estimated from video. The distance measured was from the sows shoulder to the base of the tail.

Breed	Length of Sow (cm)		
	Minimum	Median	Maximum
Duroc	87	135	174
Landrace-Duroc	136	160	188
Meishan-Landrace	87	148	217
Meishan	101	141	160

Non-behavioural Factors Influencing Mortality – confirmatory analysis

Incidence of Crushing

Crushing occurred in 50 of the 210 farrowings studied here. In 37 litters a sow crushed one piglet; in 12 litters a sow crushed two piglets; and in 1 litter a sow crushed three piglets. This crushing data was analysed using a binomial total of two - i.e. the one instance where 3 piglets from the same litter were crushed was combined with the 12 instances were 2 piglets from the same litter were crushed.

Stepwise regression fitted the following model to the crushing data:

Number of crushed piglets per litter = constant + season + length of sow + treatment + litter size + parity + length of parturition + breed

Adding a random model to this fixed model to account for repeated measures (sow/parity), divided the residual variance into sow and sow.parity strata. The amount of residual variance attributed to the sow strata was not significantly different from zero (0.000 +/- 0.948), indicating that all residual variance could be explained at the within sow level (1.174 +/- 1.157) and none at the between sow level. It was therefore applicable to analyse the 210 farrowings as independent samples, and obtain estimates for the terms in the model using the Generalised Linear Model procedure.

All of the terms in the model contributed to providing a better fit to the incidence of crushing data. Age of sow, farrowing house and cross-fostering were not included as these terms did not improve the fit of the model to the data. The residual deviance was not significant on the Chi-Square distribution (Deviance = 150.7, d.f. = 140, $p<0.50$) indicating that the model was a good fit to the crushing data.

Not all terms in the model had a significant effect on the incidence of crushing when viewed independently. An accumulated analysis of deviance looked at the effects of

added each subsequent term to the model. The addition of season (Deviance ratio, D.R. = 4.45, p = 0.004) and length of sow (D.R. = 5.19, p = 0.023) resulted in significant improvements in the fit of the data. In addition, there was a tendency (D.R. = 3.37, p = 0.067) for treatment (the presence of straw) to improve the fit of the data after accounting for season and length of sow. However, when length of sow was specified last in the model no significant effect was found on the mean number of crushed piglets per litter (p = 0.196). Similarly, when treatment was specified last in the model, the slightly higher number of crushed piglets per litter without straw (0.15; 95% Confidence Interval = 0.11 - 0.20) compared to litters with straw (0.09; 95% CI = 0.07 - 0.13) was not significant (p = 0.124).

The mean number of crushed piglets per litter was higher during the Summer months (June - August, 0.27) than during either Winter (December - February, 0.04; t_{67} = 3.09, p = 0.002) or Spring (March - May, 0.10; t_{123} = 2.20, $p<0.05$) (see Figure 5.4 for 95% confidence intervals). Whilst there was also more crushing deaths per litter during the Autumn months (September - November, 0.17) than during Winter (0.04; t = 2.10, p = 0.035). Seasonal effects on the incidence of crushing are summarised in Figure 5.4. The mean number of crushed piglets for each breed farrowing in each season are presented in Table 5.8. These means suggest that the seasonal differences shown in Figure 5.4 are independent of breed.

Figure 5.4: Seasonal differences in the incidence of crushing piglet mortalities. Mean number of crushing deaths per litter are presented, along with 95% confidence interval error bars.
** = p<0.01, * = p<0.05

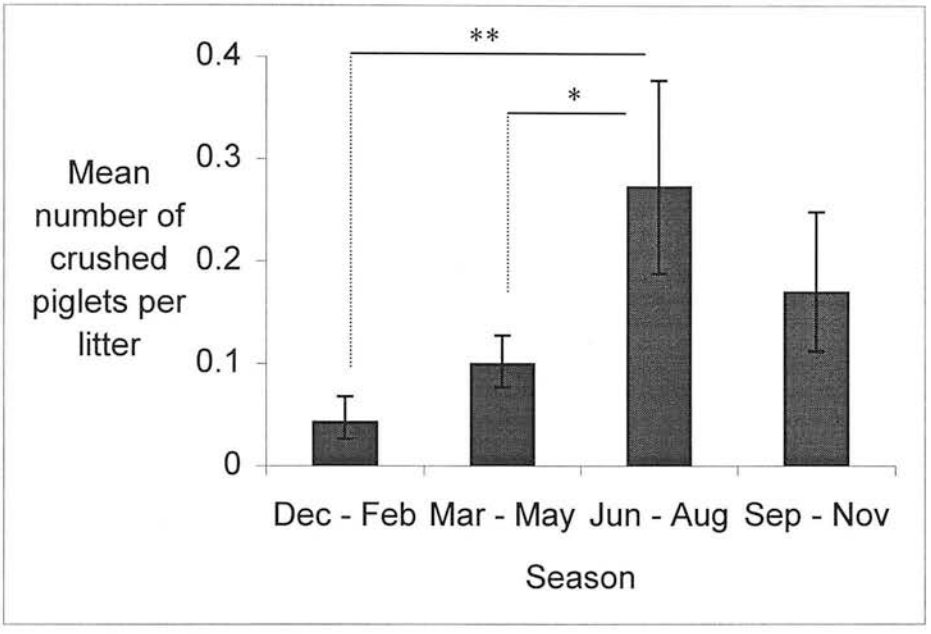


Table 5.8: Mean number of crushed piglets per litter for each breed farrowing in each season (+/- standard error). Not all breeds farrowed in all seasons, which introduced some confounding of breed with season. Sample sizes for each breed in each season can be found in Table 5.2.

	Winter	Spring	Summer	Autumn
Duroc	0.13 +/- 0.13	0.24 +/- 0.08	0.20 +/- 0.20	0.22 +/- 0.11
Landrace-Duroc	-	0.36 +/- 0.20	-	0.50 +/- 0.19
Meishan-Landrace	0.13 +/- 0.10	0.35 +/- 0.12	0.59 +/- 0.16	0.35 +/- 0.17
Meishan	0.17 +/- 0.17	0.21 +/- 0.11	-	-

After fitting all the terms in the model, there was a tendency for litter size to positively co-vary with the mean number of crushed piglets per litter ($t = 1.84$, $p = 0.065$).

Parity (p = 0.137, trend towards being lower in parity 2), length of parturition (p = 0.275) and breed (p = 0.385) had no significant effect on the mean number of crushed piglets in a litter, after accounting for all other terms in the model.

Incidence of Still-Births

Still-births were a feature of 85 farrowings of the 210 studied here. The number of litters with one, two, three and more still-births are shown in Table 5.9. The incidence of still-births was analysed using a binomial total of 3, whereby litters with three or more still-births were grouped together.

Table 5.9: The distribution of still-births amongst all gilt and sow litters.

Number of still-births	0	1	2	3	4	5	6	7	8	9
Number of litters	125	52	20	8	0	0	2	0	0	1

Stepwise Generalised Linear Regression fitted four terms to the model, in the following order:

Number of still-births per litter = constant + length of parturition + litter size + season + age of sow

Fitting a random model to this fixed model (i.e. Generalised Linear Mixed Model) to account for the repeated measures present in the data structure (sow/parity) partitioned the residual variance into sow (between sows) and sow.parity (within sows) strata. The residual variance attributed to the sow strata was not significantly different from zero (0.448 +/- 0.503), but was close to being greater than zero indicating that some of the residual variance could be explained at the within sow level. This result suggests that a degree of consistency exists, within individuals and across parities one and two, in the number of still-births per litter. Estimates for the

terms in the model were therefore obtained using the Generalised Linear Mixed Model procedure, maintaining the random model.

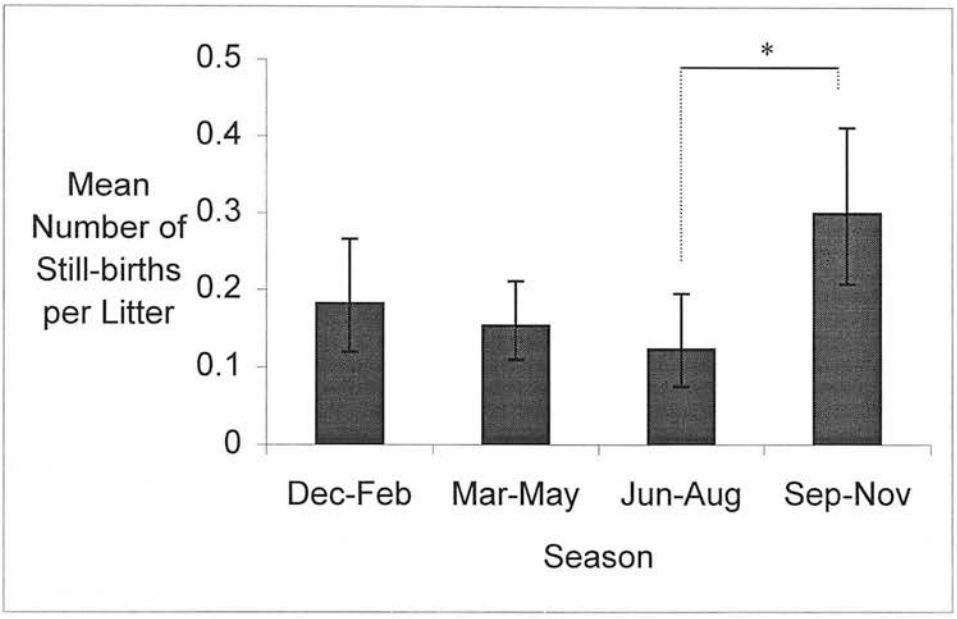
The Generalised Linear Mixed Model (GLMM) was developed further by adding other terms to the fixed model whilst keeping the same random model structure. Factors and co-variates with Wald statistics close to zero (Chi-squared distribution) were dropped from the model. Thus, parity, treatment and length of sow were dropped from the model, whilst breed and farrowing house were added to the model. The final model specified length of parturition, litter size, season, age of sow, farrowing house and breed to explain the incidence of still-births. The model was re-run several times, each time with the term of interest specified last. This ensured that differences in the mean number of still-births per litter due to the term of interest were adjusted for all other terms in the model.

There were no significant effects of breed ($p<0.50$), farrowing house ($p<0.90$), age of sow ($p<0.25$) or length of parturition ($p<0.25$) on the mean number of still-births per litter after controlling for all other terms in the model.

Litter size co-varied positively with the number of still-births (regression estimate = 0.24 +/- 0.07) ($\chi^2 = 11.3$, d.f. = 1, $p<0.001$), after controlling for all other terms in the model.

Seasonal effects on the incidence of still-births in a litter were also present after controlling for all other terms in the model. Significantly more still-births per litter were found for sows farrowing in Autumn (September - November) than in Summer (June - August) (0.30 versus 0.12; $t_{78} = 2.04$, $p<0.05$). There was also a tendency for there to be more still-births per litter for sows farrowing in Autumn than in Spring (March - May) (0.30 versus 0.15; $t_{139} = 1.76$, $p<0.10$). These seasonal differences are displayed in Figure 5.5.

Figure 5.5: The mean number of still-births per litter (+/- 95% confidence intervals) for sows farrowing during the four season. Values are back-transformed estimates from Generalised Linear Mixed Model, that controlled for repeated measures, breed, litter size, age of sow, farrowing house and length of parturition. See text for details. * = $p<0.05$



The mean number of still-births per litter for each breed farrowing in each season are presented in Table 5.10. These means suggest that the seasonal differences are independent of breed.

Table 5.10: Mean number of still-births per litter for each breed farrowing in each season (+/- standard error). Not all breeds farrowed in all seasons, which introduced some confounding of breed with season. Sample sizes for each breed in each season can be found in Table 5.2.

	Winter	**Spring**	**Summer**	**Autumn**
Duroc	1.25 +/- 0.37	0.69 +/- 0.14	0.40 +/- 0.24	1.13 +/- 0.23
Landrace-Duroc	-	0.45 +/- 0.31	-	0.25 +/- 0.16
Meishan-Landrace	0.39 +/- 0.12	0.35 +/- 0.15	0.37 +/- 0.14	0.82 +/- 0.18
Meishan	0.83 +/- 0.54	0.64 +/- 0.29	-	-

Incidence of Savaging

Savaging occurred in 12 of the 210 farrowings studied here. In 4 litters one piglet was savaged and in the remaining 8 litters two piglets were savaged. Savaging occurred too infrequently to be modelled. An attempt to model the incidence of savaging as binary data using GLMM failed due to the initial iterative process of the analysis not converging.

Incidence of Starved Piglets

Starvation was recorded as cause of death for piglets in 20 out of the 210 farrowings studied here. In 13 litters one piglet died of starvation, in 4 litters two piglets starved, in 2 litters two piglets starved and in 1 litter four piglets starved. A GLMM analysis of this data expressed as binary or using three categories of 0, 1 and 2+ starvations failed to model the data successfully, since the initial iterative process in the analysis did not converge.

Discussion

English and Smith (1975) highlighted the difficulty of attributing a single cause of death to a piglet mortality - for example, in many cases crushing may be just the secondary cause of death, with under-nutrition being the primary culprit. In addition to these difficulties, studies have shown that farm staff opinion as to cause of death have not always proved to be accurate (Palechek and McIntosh, 1993; Edwards *et al.*, 1994). Conclusions drawn from this study are sensitive to the accuracy of the farm staff reporting of the cause of piglet death. In order to try and objectify farm staff opinion of cause of death I gave the farm staff definitions of the different types of mortality. In addition mortalities that occurred during the first 24 hours following the onset of parturition were checked from video for accuracy of farm staff reporting. Given the difficulty of attributing cause of death, one solution might be to ignore the different types of mortality and analyse litter differences for total mortality (e.g. Roehe and Kalm, 2000). However, since there no clear associations between the occurrence of one type of mortality and another, this would not be a good strategy for identifying possible litter risk factors. The lack of clear associations between the different types of mortality indicates that different sows were responsible for the different types of mortality. Sows can be poor mothers for a variety of reasons, including: a) having a high propensity to savage, b) having a high propensity to crush, or c) having a high propensity to have many still-births.

The apparent independence of savaging from crushing is an important finding of this study not previously reported in the literature. The incidence of savaging amongst sows that crushed piglets was very similar to the incidence of savaging in the whole population. Signoret *et al.* (1975, p. 312) identified savaging with nervous sows that changed postures frequently, so increasing the chance of crushing a piglet. However, the results from this study do not support that assumption. It is possible that the increased risk of crushing associated with posture changing is balanced by a heightened awareness of where piglets are amongst savaging sows. These behavioural links with savaging will be explored further in Chapter 6.

There was tendency for starvation deaths to be associated with crushing deaths on a litter by litter basis, which supports the hypothesis that these two types of mortality are part of the same mortality syndrome (English and Morrison, 1984; Fraser *et al.*, 1995; English and Edwards, 1996). Standing up is a necessary activity for all sows from time to time so even sows that change postures infrequently can end up crushing piglets if they have poor milk production because poor weight gain piglets are more prone to crushing (Weary *et al.*, 1996b). Therefore, crushing and starvation mortalities can be associated with the same behavioural type of sow, even though crushing and starvation can also be viewed as alternative end points to the same process (Fraser, 1990; Fraser *et al.*, 1995).

Total mortality and pre-weaning mortality was not randomly distributed amongst the population of sows. There was a higher than expected number of litters with zero mortalities and a higher than expected number of litters with many mortalities. This supports other research indicating that some litters are more prone to mortality than others and that traits associated with the litter as a whole have a big effect on piglet mortality (Bel Isle and England, 1978; Maddock, 1980; Dyck and Swierstra, 1987; Fraser *et al.*, 1988; de Passille and Rushen, 1989; Fraser, 1990).

Exploration of the mortality data suggested that the different causes of mortality identified by farm staff should be treated separately for subsequent analyses. This created a problem when it came to modelling the less frequent mortality types. In this study it was only possible to model the incidences of stillbirths and crushings. Starvations and savagings occurred too infrequently for the Generalised Linear Modelling procedure.

In support of Roehe and Kalm's (2000) model of total piglet mortality, this study identified season as a major factor influencing both the number of stillbirths and crushed piglets. Seasonal effects on total piglet mortality have been identified by many other studies (e.g. Gracey, 1955; Pomeroy, 1960; Sadana and Singh, 1972; Nielsen *et al.*, 1974; Vrbanac *et al.*, 1995; Berger *et al.*, 1997). In this study season was found to affect crushing and stillbirth mortalities independently. Interestingly, stillbirths were more common during autumn than during summer, whilst crushings were more common during summer than during winter or spring. This suggests that

the precise seasonal effect observed in different studies of total piglet mortality will depend on the relative contributions of stillbirths and crushings to the overall mortality statistics.

Few studies have explored the reasons why seasonal differences in piglet mortality occur. The ancestor of the domestic pig, the Wild Boar, has seasonal breeding cycles, with the majority of piglets being born in the spring (Signoret *et al.*, 1975; Focardi *et al.*, 2000). Mechanisms that maintain this seasonal breeding would be adaptive since they avoid the reproductive waste of farrowing at times of year when environmental conditions would compromise the survival of piglets. Such a mechanism may act by limiting the level of maternal investment the sow puts into pregnancy, parturition and lactation at less than optimal times of year. It is possible that a mechanism like this remains in the genotype of the domestic sow, if there was no direct selection against it during domestication. Thus, domestic sows mated between December and January, for farrowing in spring, have shorter return to oestrous intervals, more piglets born alive and with greater birth weight than sows mated July-August (Xue *et al.*, 1994).

Alternatively, more proximate factors such as variation in temperature may explain the seasonal variations in piglet mortality. In this study, stillbirths were defined as a piglet either being born dead or dying within the first few minutes following birth. When faced with the challenge of thermoregulating, piglets weakened by a long delivery and with minimum glycogen reserves may not be able to respond to that challenge (English and Morrison, 1984). Therefore, many of the stillbirths observed during the colder months of the year were probably piglets that were born alive but died soon after. In this study, there were more stillbirths per litter during autumn than during summer, yet there was little difference between these seasons in the mean farrowing house temperature. In addition, there was no difference in the number of still-births per litter during winter and summer, which is consistent with what others have found (Daza *et al.*, 1999). This indicates that temperature is not an important factor influencing the incidence of stillbirths. In temperate zones, autumn represents the worst time of year to give birth to young because the entire winter season is ahead of them. Whereas, litters born in winter may have a chance of surviving through to spring if they are born towards the end of the season.

In contrast to the incidence of stillbirths, temperature does provide a reasonable proximate explanation for the higher incidence of crushing mortalities during summer than during spring or winter. In Chapter 4, data is presented showing higher frequencies of most types of sow posture change during spring, summer and autumn than during winter. A high frequency of posture changing has previously been associated with a high incidence of crushings (Edwards *et al.*, 1986; Weary *et al.*, 1996a). Also presented in Chapter 4, was data showing that piglets born during the summer spend less time in the creep than piglets born during spring, suggesting that piglets in the summer are more at risk from crushing than piglets born during the spring. These relationships between sow behaviour, piglet behaviour and piglet crushing will be explored in later Chapters.

In line with what other studies of piglet mortality have found, the number of still-births per litter increased with litter size, whilst the number of crushing mortalities also tended to increase with litter size (Fahmy and Bernard, 1971; Sadana and Singh, 1972; Nielsen *et al.,* 1974; Bille *et al.*, 1974; Edwards *et al.*, 1986, 1994; de Passille and Rushen, 1989; Weary *et al.*, 1998). A large litter size can increase the risk of mortality through at least four interrelated mechanisms: (1) large litters will tend to have a higher proportion of low birth weight and reduced viability piglets (Edwards *et al.*, 1994); (2) these small piglets will be further weakened through the increased risk of anoxia caused by the cumulative effects of successive contractions (Edwards *et al.*, 1994; English and Edwards, 1996); (3) large litters are associated with increased competition for teats (Fraser, 1975); (4) large litters are associated with and an increased probability of crushing (Weary *et al.*, 1998). These mechanisms predict a strong association between crushing and litter size, however there was only a weak effect of litter size on the number of crushings ($p = 0.065$). This suggests that an additional factor, such as the behaviour of the sow, intervenes to weaken the association between litter size and crushing.

Interestingly, length of parturition was not an independent factor influencing the incidence of stillbirths. Although a higher incidence of stillbirths was found in litters with longer parturitions, as others have found (e.g. Randall, 1972; Fraser *et al.*, 1997), after controlling for season, breed, litter size, farrowing house and age of sow, this apparent effect disappeared. The majority of the between litter variation in the number

of stillbirths was explained by differences in litter size, a factor that the previous studies did not control for.

There were no effects of breed on the incidence of crushed piglets or the incidence of still-births, once factors linked to breed such as season, litter size, length of parturition and length of sow had been controlled for. This suggests that genetic influences on the incidence of still-births and crushings must be present in all four breeds studied here. The number of stillbirths and crushings positively co-varied with litter size, which is known to have a good heritability (e.g. Wang *et al.*, 1994), suggesting that mortality might be reduced if the selection pressure for litter size was reduced. In this study, there was some evidence of a sow's likelihood of having stillbirths being consistent over the first two parities, suggesting that this is a stable maternal trait. In contrast, there was no evidence that sows were consistent over their first two parities in their likelihood to crush piglets. Previous research has found only a low repeatability for the number of stillbirths per sow (Siewerdt and Cardellino, 1998), and low heritabilities for piglet mortality (Kerr and Cameron, 1995; van Arendonk *et al.*, 1996; Roehe and Kalm, 2000). Low heritabilities are expected for traits that are strongly related to fitness (Redei, 1982).

Parity did not influence the number of still-births, which supports the previous finding that sows were consistent over parities one and two in their number of still-births. There was also no significant effect of parity on the number of crushed piglets per litter, however, in this case this was not due to sows being consistent. These findings are consistent with other studies since parity effects on both stillbirths and mortality during lactation only reveal themselves when low parity sows (e.g. parities one to three) are compared with high parity sows (e.g. four and above) (Nielsen *et al.*, 1974; Daza *et al.*, 1999; Roehe and Kalm, 2000).

There was no significant effect of straw on the occurrence of either stillbirths or crushing mortalities, which supports the results of Edwards and Furniss (1988). This finding is in contrast to the situation in outdoor pig production where the amount of straw in the farrowing hut has been found to be negatively correlated to the percentage of piglet mortality (Berger *et al.*, 1997). Thus, it would appear that the

benefits of straw to piglet survival in outdoor systems are probably thermoregulatory, which is unimportant in indoor systems where heat lamps keep the piglets warm.

Summary and Conclusions

1. Stillbirth was the most frequent cause of piglet death amongst crated sows and gilts, followed by crushing.
2. The distributions of total piglet mortality and total pre-weaning mortality amongst litters were not random. There was a higher than expected number of litters with zero mortalities and a higher than expected number of litters with three or more mortalities. This indicates that some litters are more prone to mortality than others, which supports the findings of other studies (Bel Isle and England, 1978; Maddock, 1980; Dyck and Swierstra, 1987; Fraser *et al.*, 1988; de Passille and Rushen, 1989; Fraser, 1990).
3. There were no significant associations between the occurrence of one type of mortality and another within litters. However, there was a tendency for starvation mortalities to be associated with crushing mortalities, which supports the hypothesis that these two mortality types are part of the same syndrome (English and Morrison, 1984; Fraser *et al.*, 1995; English and Edwards, 1996).
4. Season was a major factor influencing the number of stillbirths and crushings per litter, which is consistent with many other studies. There were more stillbirths in autumn than in summer, indicating that an evolved mechanism for conserving reproductive investment may be present in the domestic sow genotype. There were more crushings in summer than in spring and winter. The higher temperatures in summer, increasing the frequency of sow posture changing and the time piglets spend out of the creep (Chapter 4), would seem to be responsible for the seasonal effects on piglet crushing.
5. Litter size positively co-varied with both the number of stillbirths per litter ($p<0.001$) and the number of crushed piglets per litter ($p = 0.065$), which is consistent with the background literature (Fahmy and Bernard, 1971; Sadana and Singh, 1972; Nielsen *et al.,* 1974; Bille *et al.*, 1974; Edwards *et al.*, 1986, 1994; de Passille and Rushen, 1989; Weary *et al.*, 1998). Litter size can affect piglet mortality through several interrelated mechanisms, but the lack of a strong association between crushing and litter size suggests that an additional factor, such as the behaviour of the sow, modifies the relationship between crushing and litter size.

6. Length of parturition appeared to be an important covariate influencing the incidence of stillbirths, which supported the findings of others (Randall, 1972; Fraser *et al.*, 1997). However, after controlling for litter size, length of parturition did not have a significant influence on the number of stillbirths per litter.
7. Breed did not explain any of the litter differences for both the number of crushing mortalities and the number of stillbirths, indicating any genetic influences on the incidence of these mortalities must be present in all the breeds studied here. This study uncovered no evidence of any genetic influences on the incidence of crushing, since sows were not consistent over parities one and two in whether they crushed or not. In contrast, there was evidence of a small degree of consistency, over the first two parities, for a sows likelihood of having stillbirths. Consistency in the expression of a trait indicates that the trait might be heritable.
8. There were no significant differences between parity one and two in the number of stillbirths or crushings, which supports the findings of others (e.g. Nielsen *et al.*, 1974; Daza *et al.*, 1999; Roehe and Kalm, 2000).
9. Straw did not influence the number of stillbirths or crushings in the farrowing crate, which is consistent with what Edwards and Furniss (1988) found.

CHAPTER 6:

BEHAVIOURAL CHARACTERISTICS OF SAVAGING SOWS AND HOW THESE INFORM ON FUNCTIONAL AND CAUSAL MECHANISMS

Introduction

Savaging by sows (sometimes called cronism, cannibalism or own offspring maternal infanticide) makes a small but significant contribution to the overall pre-weaning mortality statistics (Chapter 5). A very small proportion of sows (5.7%) were responsible for all of the savaging deaths (Chapter 5). Understanding why these few sows savage should allow substantial progress to be made towards reducing the incidence of savaging under commercial conditions.

Savaging tends to occur during a sows first parturition (van der Steen *et al.*, 1988). The killing of offspring in a captive environment has often been viewed as a non-adaptive pathological behaviour brought on by various aspects of the artificial environment (Eisenberg, 1981: p. 398; Fraser and Broom, 1990, p. 223). Fraser and Broom (1990, p. 341) state that the origin of piglet-directed aggression and savaging lies in the behavioural mechanisms that lead to defence of the young in the wild. However, they offer no evidence to support this theory. Others have suggested high rates of piglet mortality are a consequence of evolved reproductive strategies relating to brood reduction, either through sibling competition (Fraser, 1990) or through direct maternal intervention (Harris *et al.*, 2000).

Sambraus (1976, 1985) identified three types of piglet-savaging behaviour in sows (summarised by Fraser and Broom, 1990): (a) where accidentally crushed piglets are eaten or partially eaten; (b) where the sow actively avoids her piglets and directs aggression towards piglets that approach her; (c) where the sow is actively aggressive

to both humans and piglets and usually kills the entire litter (Fraser and Broom, 1990, p. 341).

Adaptive brood reduction is common in many species of bird (see Mock, 1984 for a review) and occurs when the environment, in particular, the abundance of food in the environment, is inadequate to successfully rear the whole brood (O'Connor, 1978). The mechanism by which brood reduction occurs in birds is usually sibling competition (Mock, 1984). Brood reduction enhances the fitness of the survivors and improves the mothers ability to invest in future broods (Howe, 1976; O'Connor, 1978; Tait, 1980; Gosling, 1986; Lloyd, 1987; Parker and Mock, 1987 - all cited by Clutton-Brock, 1991). When larger chicks monopolise food resources, the parents failure to intervene may either be an evolved strategy or a consequence of being unable to regulate the sibling competition effectively (Clutton-Brock, 1991).

In polytocus mammals, such as rodents and pigs, the mechanism of brood reduction is sometimes different. In rodents there is clear evidence that own offspring maternal infanticide can sometimes occur. The rodent mother will reduce her brood size in cases where energetic burdens or the risk of infanticide by intruder males is high (Day and Galef, 1977; Gandelman and Simon, 1978; Fuchs, 1982; Huck, 1984; Bronson and Marsteller, 1985; Perrigo, 1987; Mendl, 1988 - cited in Clutton-Brock, 1991). Species differences exist for maternal own-offspring infanticide. In house mice the female kills some of her young soon after birth, whereas in deer mice, entire litters are killed but rarely individual pups (Perigo, 1987). It is not known whether own offspring maternal infanticide exists as an adaptive strategy in wild pigs but when forced to farrow in straw pens, wild sows will occasionally savage their piglets (Harris *et al.*, 2000). This illustrates that wild pigs are capable of savaging piglets, however it does not provide proof that it is an adaptive strategy employed by sows in the wild as there is no evidence that wild pigs will savage their young under 'natural' ecological conditions. This result from Harris *et al.* (2000) does not remove the possibility that savaging is merely a maladaptive response to some aspect of the captive environment.

One assumption of the adaptive brood reduction hypothesis of savaging is that the environment is in someway perceived as being too poor to successfully rear a whole

litter of piglets. In wild populations, poor environments resulting in brood reduction usually mean low food abundance (O'Connor, 1978; Mock, 1984) but this is rarely the case for lactating sows on farms. The aim on farms is always to maximise milk production by providing sows with enough digestible energy and crude protein to support their litters (Varley, 1995), so lactating sows and gilts are usually fed *ad libitum*.

Food availability is not the only aspect of the captive environment whereby a perceived inadequacy could prompt a brood reduction strategy. The captive environment might be full of cues that could be perceived as inadequate for the rearing of young, for example freedom of movement or the lack of a nest. However, many of these cues will be specific to the captive environment and absent from the sows evolutionary history, preventing the sow from making the connection between, for example, lack of freedom of movement and reduced likelihood of being able to rear all her litter. On the other hand, other aspects of the captive environment, such as being disturbed by a human intruder, might be perceived as being equivalent to being disturbed by a predator in the wild, and an evolved strategy might be employed to respond to this disturbance. In environments where disturbance by a predator is common, wild animals will sometimes desert entire broods, reabsorb developing foetuses or eat their whole litter (Bradbury and Vehrencamp, 1977; Mock, 1984; Gosling, 1986). However, this is not classed as a brood reduction strategy.

If savaging behaviour is not an adaptive behaviour, designed to maximise the lifetime reproductive success of the sow, then it must be maladaptive since it results in a decrease in the sows reproductive success. It is possible that savaging might be a consequence of the farming conditions and the inherent constraints associated with captivity. For example, on farms, pigs are usually reared in groups of similar age and so the first experience a gilt will have of piglets will be when she gives birth to her first litter. Whereas in the wild, pigs are found in family groups and young gilts will have experienced different ages and sizes of pigs before giving birth herself. In light of novelty being a causal factor of savaging, some farmers have taken to putting domestic rabbits in the farrowing crates of gilts to allow them to habituate to small novel animals (anonymous, 1997 - article from Pig International). However, if novelty was the only factor responsible for savaging then savaging should be seen just as

frequently in farrowing pens as in farrowing crates but this does not appear to be the case (Cronin *et al.*, 1996). Therefore, if novelty is important it is probably only one of several contributing factors in the aetiology of savaging. The novel experience of seeing piglets for the first time, combined with the pain associated with giving birth (Jarvis, 1997) and the stress caused by having movement restricted (Lawrence *at al.*, 1994; Boulton *et al.,* 1997a), might trigger piglet savaging behaviour. This hypothesis would predict that:

a) savaging only occurs in gilts without previous experience of piglets
b) gilts that are more sensitive to the stressor of being restricted would be more likely to savage their piglets.

Identifying individuals that are more sensitive to the stressor of being restricted is complicated using behavioural observation alone, making the second prediction above difficult to test in the current study. However, by looking at the behavioural effects of restriction we can predict how sows and gilts hyper-sensitive to the stressor of restriction would react. Sows farrowing in crates have a greater activation of the Hypothalamic-Pituitary-Adrenal (HPA) system during the pre-farrowing period compared to sows farrowing in pens (Lawrence *et al.*, 1994; Jarvis *et al.*, 1997). Heightened opioid tone is thought to occur concurrently with HPA activation (Laatikainen, 1991), in response to various environmental stressors (Amir *et al.*, 1980; Lawrence *et al.*, 1997). One of the roles of endogenous opioids is the inhibition of oxytocin release, through both auto-inhibition at the oxytocin nerve terminals of the pituitary and at pre-synaptic receptors in the supraoptic nucleus (Douglas *et al.*, 1993, 1995; Onaka *et al.*, 1995; Lawrence *et al.*, 1997). In addition, oxytocin is also prevented from being released by progesterone intensifying the actions of the inhibitory neurotransmitter Gamma-Aminobutyric Acid (GABA), and through the release of nitric oxide from oxytocin neurones (Russell, 2000). It has been suggested that a chronically high opioid tone can desensitise the crated sows oxytocin system to opioid inhibition (Lawrence *et al.*, 1995; Lawrence *et al.*, 1997). The cause of heightened HPA activation and associated opioid tone in crated sows is thought to be the thwarting of nest-building behaviour (Lawrence *et al.*, 1997). Therefore, as the motivation to nest-build dissipates and progesterone secretion collapses near term (Russell, 2000), the crated sow sensitive to restriction will be left with insufficient restraint of oxytocin release from the pre-synaptic receptors of the supra-optic

nucleus. The resulting surge of oxytocin will act on the smooth muscle of the myometrium (Higuchi *et al.*, 1986; Russell, 2000) causing an initial high rate of piglet expulsion. High concentrations of oxytocin have been observed in sows farrowing in crates compared to sows farrowing in pens (Lawrence *et al.*, 1995). If piglet-savaging sows reflect an extreme case of sensitivity to restriction then we would expect to see a high rate of piglet expulsion from savaging sows compared to non-savaging sows. A high rate of piglet expulsion will result in the relatively sudden appearance of many piglets compared to sows with better opioid restraint of oxytocin release, which, in turn will act to promote any effect of novelty of the piglet stimuli.

It is important to note that the causal hypothesis outlined above does not directly compete with the functional hypothesis of adaptive brood reduction. However the two hypotheses differ in their predictions of when savaging will occur. The brood reduction hypothesis predicts that savaging would be more common:

a) in large litters
b) at times of food restriction and that
c) brood reduction would act on the weakest piglets in the litter.

The present study was designed to test the predictions of the adaptive brood reduction hypothesis of savaging, whilst using the natural variation between litters to identify potential causal factors for piglet savaging.

Methods

Experimental Design

The experiment was based around a breed by parity by treatment factorial design whereby individual sows were observed over two parities. The design was unbalanced largely as a result of sows 'dropping out' between parities (see chapter 2). Treatment was the presence or absence of straw that was allocated randomly within breeds (see chapter 2).

Behavioural Observations

Sows and gilts were observed during 10-minute samples at -24, -20, -16, -14, -12, -10, -8, -6, -4, -2 and 0 hours pre-farrowing. And from the birth of the first piglet (BFP) for six hours continuously and then for a further six 10-minute samples at 9, 12, 15, 18, 21 and 24 hours (see chapter 2). The pre-farrowing behaviour of sows and gilts was summarised as four time blocks: -24, -20 hours; -16 to -12 hours; -10 to -6 hours; -4 to 0 hours. The behaviour of sows and gilts following the birth of the first piglet was summarised as seven 60-minute time intervals, six from the six hour sample and one from collating information from the time samples at 9, 12, 15, 18, 21 and 24 hours.

Piglet behaviour and location was measured on a whole litter basis using scan samples every 5 minutes following the onset of parturition and during the sow observation times. This data was summarised as for the sow and gilt behaviour.

Statistical Analysis

Observations were made from 96 parity one gilt farrowings and 63 parity two sow farrowings. In 57 cases the same individual was observed over both parities. Out of these 159 farrowings, 11 litters, all from parity one gilts, contained at least one piglet that had been savaged by its mother (classed as savaging sows (SS)). In addition to

the 11 savaging gilts, there were also 41 gilts and sows that, although not savaging a piglet to death, were seen either biting or snapping at piglets (see Chapter 2 for definitions) during the behavioural observation periods (classed as non-savaging but aggressive sows (NA)). In 107 sow and gilt farrowings, no biting, snapping or savaging was seen and no piglets were recorded as being killed through savaging (classed as non-savaging and non-aggressive sows (NN)).

Behaviours measured as frequencies (events) were transformed to the logarithmic scale, and behaviours measured as proportions (states) were transformed using the arcsine-square-root transformation. These transformations succeeded in making most of the behavioural measures fit the requirements of parametric tests. Post-hoc analysis of residuals and fitted values were used to check whether the data fulfilled parametric criterion.

The behaviour of these three groups of sows (SS, NA, NN) was analysed for differences in their behaviour using a combination of Canonical Variates Analysis (CVA) and Restricted Maximum Likelihood tests (REML). The CVA was used to identify behaviours most likely to distinguish between the groups and so limit the number of behaviours that needed to be modelled using REML. Canonical variates analysis produces orthogonal canonical variates, a combination of all behavioural measures, which describe the variation between the group means. The loadings on each behavioural measure are correlated to the importance of each behaviour in discriminating between the groups.

REML was chosen because of its ability to deal with unequal group sizes. The fixed model specified in the analyses included all experimental (e.g. breed, treatment, parity) and non-experimental factors that varied between litters (e.g. season, farrowing house, time of day, see Chapters 3 and 4 for a complete list). Litter size and age of sow were included as covariates and savaging group was specified last, thereby controlling for all other factors. Repeated measures on sows over the two parities were accounted for by nesting parity within sow in the random model (sow/parity). The REML tests produced Wald Statistics (W), based on the Chi-squared distribution, and estimated means and standard errors. Differences between savaging group means were identified using the standard error of the difference to generate t-statistics.

A Wilcoxon-signed-rank test was used to investigate whether birth intervals prior to the onset of piglet-directed aggression were shorter than birth intervals after the onset of piglet-directed aggression. Non-parametric analysis was necessary due to the inequality of variance between the birth intervals before and after the onset of aggression. This comparison was only possible for gilts that began behaving aggressively after the second piglet was born (otherwise there would be no pre-aggression birth interval). The mean birth interval length prior to the first sign of aggression was compared to the mean birth interval length after the first sign of aggression. This was done by calculating the difference between birth intervals before and after aggression (e.g. mean after - mean before) for each animal and ranking these values regardless of sign. The sum of ranks for positive signed differences and negative signed differences was then calculated. If birth intervals were similar before and after aggression, the two sums of ranks will be similar. Thus the smaller of the two ranks can be compared with a set of critical values in a Wilcoxon statistical Table, to see if the two groups were significantly different. To ensure that a systematic time error was not responsible for differences in birth interval length before and after first sign of aggression, mean birth intervals were plotted for the course of parturition.

Mann-Whitney U-tests (Siegel, 1956) were used to compare the birth intervals for savaging gilts prior to the onset of first aggression, with equivalent birth intervals for non-savaging gilts. This was done by randomly selecting a matched pair for each savaging gilt, within breed, season of farrowing and litter size. Breed, season and litter size have been previously shown to influence birth intervals (Chapter 4, p. 80). If the first instance of aggression occurred after the fourth piglet was born, a mean birth interval was calculated from the first three birth intervals for both the savaging gilt and its matched pair. This calculation was repeated for each savaging gilt not showing piglet-directed aggression until after the second piglet was born. As before, non-parametric statistics were necessary due to inequality of variance between the samples. The Mann-Whitney U-test uses a ranking procedure to compare data from two independent groups.

Pearson product moment correlations were calculated to explore relationships between different types of piglet-directed behaviour.

Results

Piglet-directed Aggression in Savaging and Aggressive Sows

Piglet-directed aggression was recorded as bite (sow lunges towards piglet with mouth open and closes her mouth around the piglet) and snap events (sow lunges towards piglet with mouth open but does not close her mouth around the piglet). The mean number of snap and bite events for savaging (SS) and non-savaging aggressive sows are shown in Table 6.1.

Table 6.1: Mean number of bites and snaps per hour (+/- standard error) for savaging and non-savaging aggressive sows (as defined in this study).

Aggressive event	Savaging (SS)	Non-savaging, aggressive (NA)
Bite	0.45 +/- 0.11 bites per hour	0.03 +/- 0.02 bites per hour
Snap	1.22 +/- 0.53 snaps per hour	0.24 +/- 0.02 snaps per hour

Straw and Breed Effects on the Occurrence of Savaging

Savaging occurred too infrequently to discriminate the effects of breed and straw on the incidence of savaging for the confounding effects of other factors that differed between litters (see Chapter 5).

There was a higher incidence of savaging amongst Duroc gilts compared to the other breeds, however it is not known whether this is an effect of season or litter size. The occurrence of savaging did not appear to be influenced by the presence of straw but this could also be due to confounding factors (see Table 6.2).

Table 6.2: The occurrence of farrowings with savagings amongst the four genotypes with or without straw in the farrowing crate.

Breed	Treatment	
	Straw	No Straw
Duroc	3 (10%)	4 (16%)
Landrace-Duroc	0	0
Meishan-Landrace	1 (2.6%)	2 (6.1%)
Meishan	1 (11%)	0

Progress of Parturition and The Occurrence of First Aggression

In all cases, piglet-directed aggression began before parturition finished (see figure 6.1). In four out of eleven cases, the first sign of aggression came before the second piglet was born. For the remaining seven gilts it was possible to compare mean birth intervals before and after the onset of aggression.

The mean of all birth intervals prior to first act of piglet-directed aggression (9.4 +/- 4.3 minutes) was shorter than the mean of all birth intervals following the first act of piglet-directed aggression (66.8 +/- 38.6 minutes, Wilcoxon matched pairs, $W = 1$, $N = 7$, $p<0.05$).

A comparison between the mean birth intervals prior to the onset of aggression in savaging gilts and equivalent birth intervals in non-savaging gilts (randomly selected matched pair, selected within breed, litter size and season – see Methods) found a tendency for savaging gilts to have a faster rate of parturition prior to aggression (Mann-Whitney, $U = 13$, $n_1 = 7$, $n_2 = 7$, $p = 0.082$).

Figure 6.1: The occurrence of the first instance of piglet-directed aggression (snap and bite events and savaging bout) and the mean length of parturition for the 11 savaging gilts (+/- standard error).

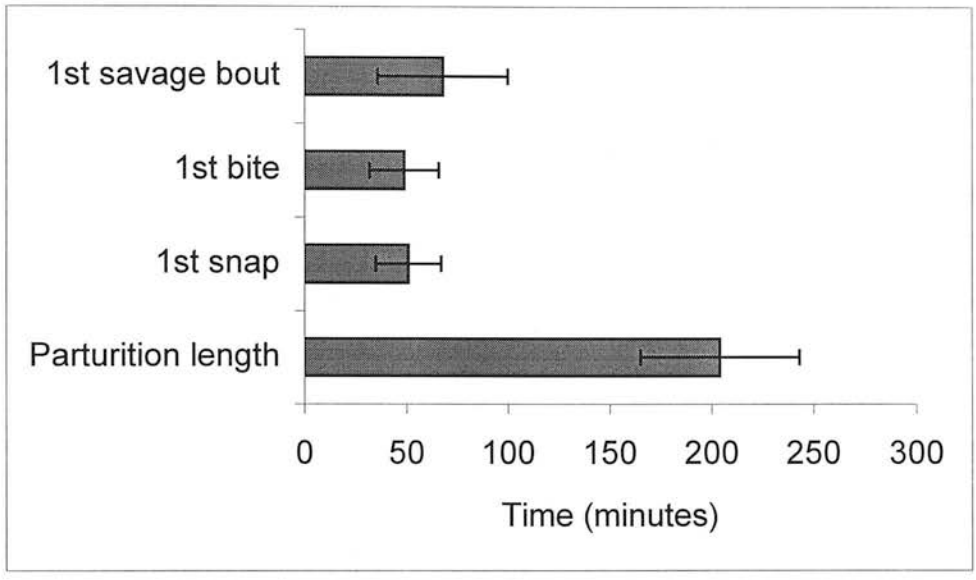
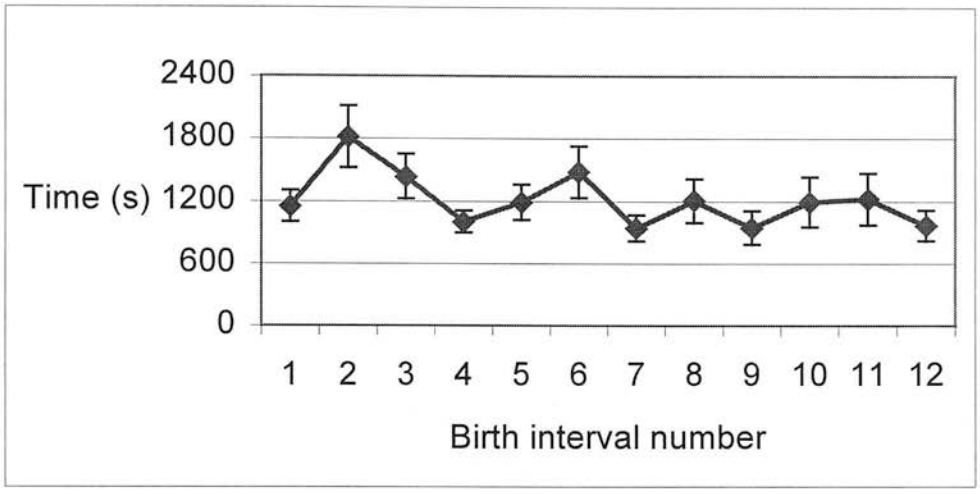


Figure 6.2 illustrates how birth interval length changed over the course of parturition for all of the gilts studied here, including the savaging gilts. There was no linear relationship between the progress of parturition and mean birth interval length. This was true for all breeds (although only means for all breeds combined are shown in the graph). Therefore the onset of aggression is associated with a slowing of parturition and a lengthening of birth intervals, which would not have otherwise happened. The apparent slight decrease in mean birth interval as parturition progresses (figure 6.2) was due to the later birth intervals coming from the more prolific breeds (Meishan and Meishan-Landrace), that had shorter birth intervals and shorter parturitions (see Chapter 4).

The mean birth interval length over the first 12 intervals and for all breeds combined was 20.2 +/- 1.2 minutes.

Figure 6.2: Mean birth intervals of all parity one gilts (savaging and non-savaging gilts) (n = 96).



Litter size had no clear effect on the occurrence of either the incidence of savaging or piglet-directed aggression (see Table 6.2).

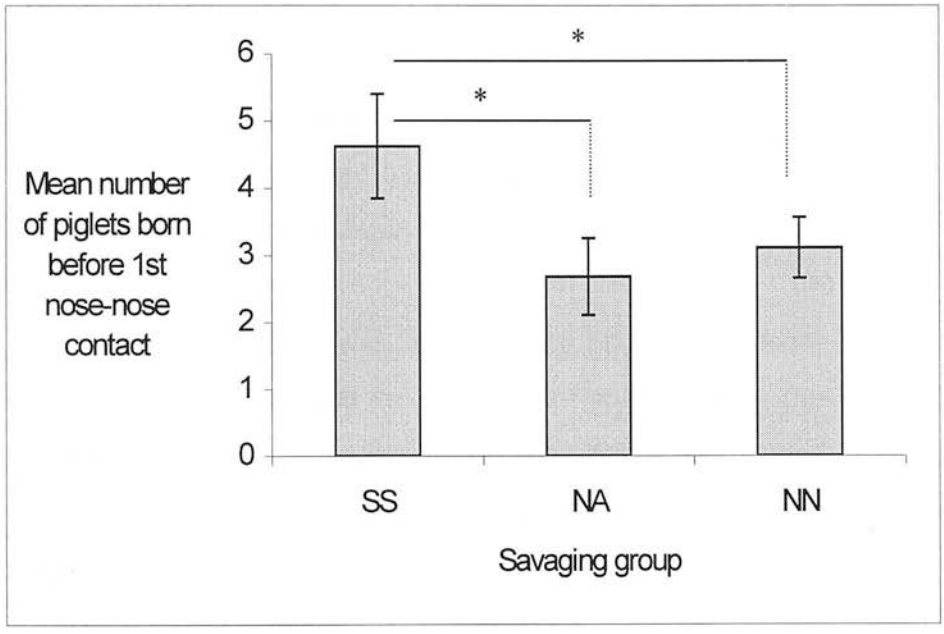
Table 6.2: Mean parity one litter size per breed and per savaging group. Within each breed, means with different superscripts denote significant differences at $p<0.05$ (t-distribution).

Breed	**Mean litter size (+/- standard error) per savaging group and group sample size**					
	Savaging		Non-savaging, aggressive		Non-savaging, non-aggressive	
	n	mean	n	Mean	n	Mean
Duroc	7	10.1 +/- 1.1[a]	8	9.1 +/- 0.6[a]	16	9.4 +/- 0.5[a]
Landrace-Duroc	0	-	5	12.0 +/- 0.5[a]	6	9.3 +/- 1.3[b]
Meishan-Landrace	3	9.7 +/- 0.7[a]	10	11.9 +/- 0.7[b]	24	10.3 +/- 0.4[ab]
Meishan	1	10.0	6	11.5 +/- 1.1[a]	10	12.7 +/- 1.0[a]

The latency before first nose-nose (2691 +/- 228 seconds) or nose-body (2575 +/- 212 seconds) sow-piglet contact was subject to considerable variation between sows.

Neither of these two measures differed significantly between the savaging groups. However, the mean number of piglets born prior to the first nose-nose contact was higher for savaging sows than for either non-savaging but aggressive (t_{50} = 2.6, $p<0.02$) or non-savaging, non-aggressive sows (t_{116} = 2.4, $p<0.02$) (see figure 6.3).

Figure 6.3: Mean number of piglets born (+/- standard error) prior to first nose to nose sow-piglet contact. SS = savaging sows (n = 11), NA = non-savaging but aggressive sows (n = 41), NN = non-savaging non-aggressive sows (n = 107). Values are adjusted for repeated measures and controlled for parity, breed, season, age of sow, whether straw was present, time of day, farrowing house, whether a radio was on in the farrowing house, litter size and whether drugs were administered. * = $p<0.05$



The age of parity one gilts on the day of parturition varied from 279 days to 529 days (mean = 390 +/- 5 days). Initial inspection of the age of savaging gilts seemed to indicate that savaging was more common amongst younger gilts, whilst piglet-directed aggression without savaging did not appear to be affected by age (see Table 6.3).

Table 6.3: The occurrence of savaging and piglet-directed aggression without savaging in four gilt age groups.

Age of Gilt (days)	Sample size	Percentage that Savage	Percentage that show piglet-directed aggression but do not savage
< 350	19	21.1	26.3
350 - 399	38	0.8	23.7
400 - 449	30	1.0	33.3
> 449	9	11.1	55.6

However, since the four breeds differed in their age at first parturition (Duroc - 359.7 +/- 6.9; Landrace-Duroc - 401.1 +/- 3.4; Meishan-Landrace - 420.9 +/- 6.8; Meishan - 411.6 +/- 21.4), it was necessary to look within breeds for an age effect. Savaging was rare and so an effect of age on savaging could only be analysed within one breed, Duroc (see Table 6.2 for sample sizes).

Within Duroc gilts, there was no difference between the mean age of savaging gilts (SS, 350.4 +/- 6.1 days) and the mean age of non-savaging gilts (NA + NN, 357.0 +/- 4.2 days). However, aggressive Duroc gilts (SS + NA) tended to be younger (350.3 +/- 4.9 days) than non-aggressive Duroc gilts (NN, 360.5 +/- 4.9, $t_{28} = 1.44$, $p = 0.076$).

Behavioural Differences Between Savaging and Non-savaging Sows and their Litters

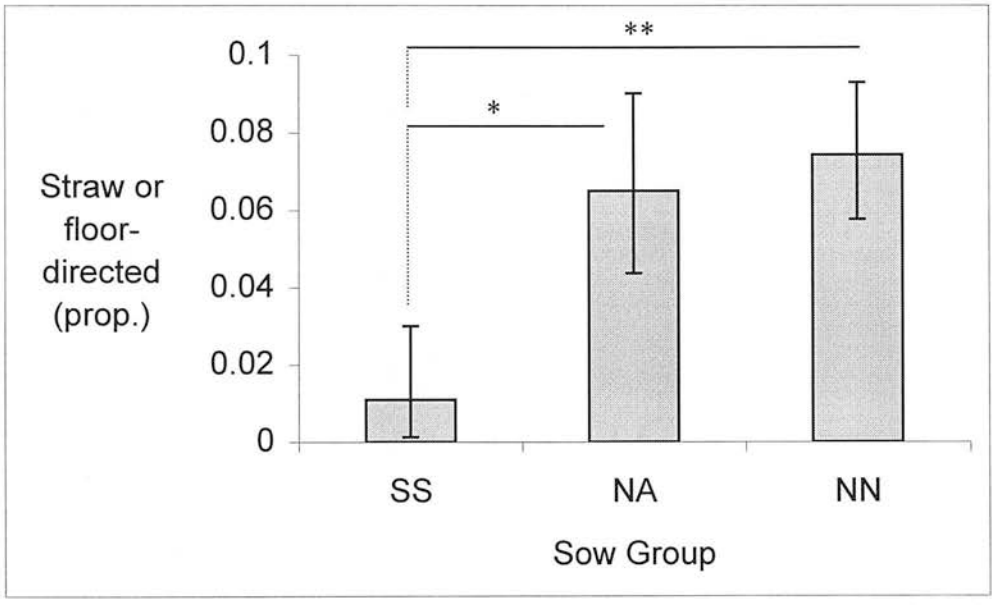
i) Pre-farrowing

Behavioural differences between the savaging groups were found during two time blocks during the 24 hour pre-farrowing period. These were -16 to -12 hours and -4 to 0 hours pre-farrowing. There were no behavioural differences between savaging and

non-savaging sows between -24 and -20 hours and between -10 and -6 hours pre-farrowing.

During the run up to peak nest-building, -16 to -12 hours, the majority of sows spent increasing proportions of their time in straw or floor-directed behaviour. Savaging sows, on the other hand, were observed doing much less straw or floor-directed behaviour than either non-savaging, non aggressive (t_{116} = 3.0, $p<0.01$) or non-savaging, aggressive gilts (t_{50} = 2.2, $p<0.05$) (see figure 6.4).

Figure 6.4: Proportion time spent in straw/floor-directed behaviour between -16 and -12 hours pre-farrowing, for savaging (SS, n = 11), non-savaging but aggressive (NA, n = 41) and non-savaging, non-aggressive gilts (NN, n = 107). Values are adjusted for repeated measures and controlled for parity, breed, season, age of sow, whether straw was present, time of day,

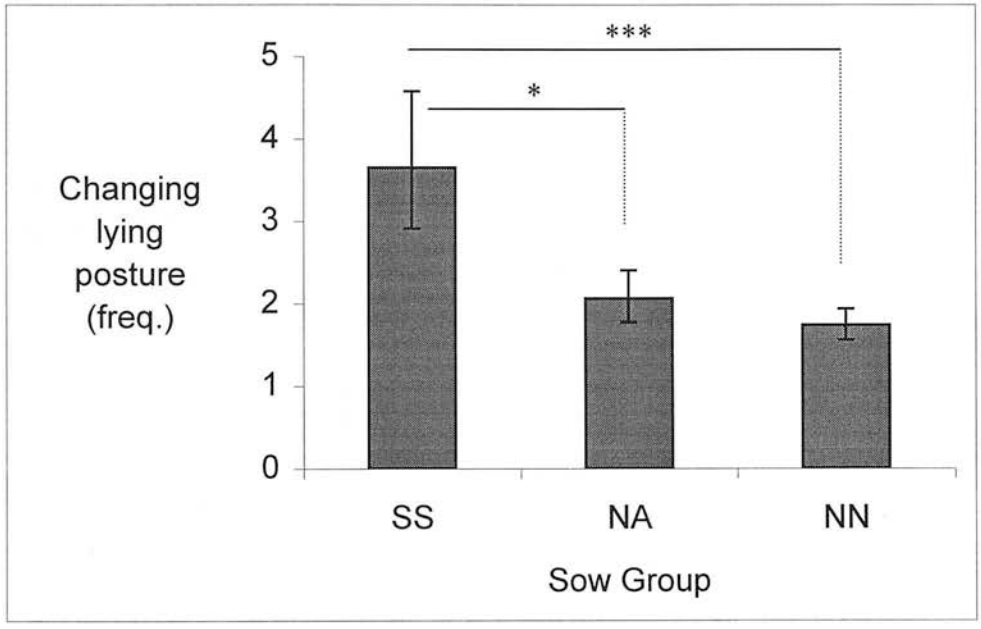


farrowing house and whether a radio was on in the farrowing house. Error bars show the 95% confidence intervals. ** = $p<0.01$, * = $p<0.05$

During the same time period, -16 to -12 hours, savaging gilts spent more time lying ventrally (57.3%, 95% CI = 46.4 - 67.8) than non-savaging aggressive sows and gilts (32.9%, 95% CI = 26.2 - 39.9; t_{50} = 2.2, $p<0.05$) and non-savaging non-aggressive sows and gilts (32.1%, 95% CI = 27.2 - 37.0; t_{116} = 2.9, $p<0.01$).

Also between -16 and -12 hours (30 minutes of observation) savaging sows changed lying posture more frequently than non-savaging aggressive sows ($t_{50} = 2.6$, $p<0.02$) and non-savaging, non-aggressive sows ($t_{116} = 4.1$, $p<0.001$) (see figure 6.5).

Figure 6.5: Mean frequency of changing posture whilst lying (+/- 95% confidence interval) between -16 and -12 hours pre-farrowing (30 minutes of observation). Groups along the x-axis represent savaging (SS), non-savaging but aggressive (NA) and non-savaging, non-aggressive sows (NN). Values are adjusted for repeated measures and controlled for parity, breed, season, age of sow, whether straw was present, time of day, farrowing house, whether a radio was on in the farrowing house.
*** = $p<0.001$, * = $p<0.05$



The next instance when savaging sows could be differentiated from non-savaging sows on the basis of their pre-farrowing behaviour was during the time sample just prior to parturition, -4 to 0 hours. During this time period, savaging gilts spent less time sitting than non-savaging but aggressive sows and gilts ($t_{50} = 2.4$, $p<0.02$) and non-savaging, non-aggressive sows and gilts ($t_{116} = 2.9$, $p<0.01$) (see figure 6.6). Savaging gilts also spent more time standing (17.2%, 95% CI = 10.8 - 24.7) than non-savaging, non-aggressive sows and gilts (7.1%, 95% CI = 5.0 - 9.5; $t_{116} = 2.1$, $p<0.05$).

During the same time period, savaging sows spent a more time mouthing the crate fixtures than non-savaging, non-aggressive sows ($t_{116} = 3.0$, $p<0.01$) (see figure 6.7).

Figure 6.6: Mean proportion time spent sitting (+/- 95% confidence interval) between -4 and 0 hours pre-farrowing, for savaging (SS), non-savaging but aggressive (NA) and non-savaging, non-aggressive gilts (NN). Values are back-transformed REML estimates, adjusted for repeated measures and controlled for parity, breed, season, age of sow, whether straw was present, time of day, farrowing house, whether a radio was on in the farrowing house. ** = $p<0.01$, * = $p<0.05$

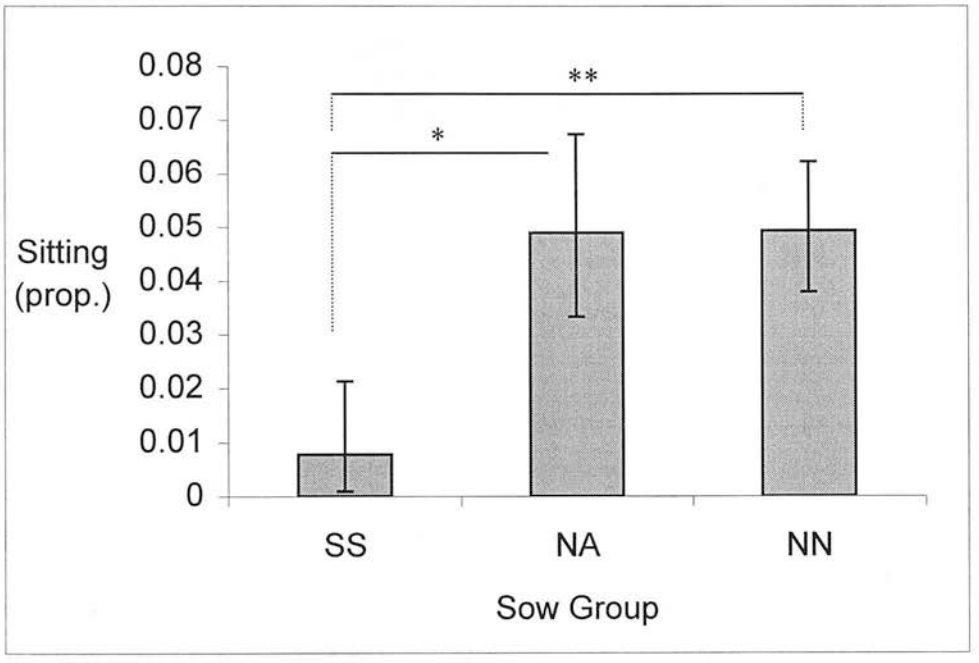
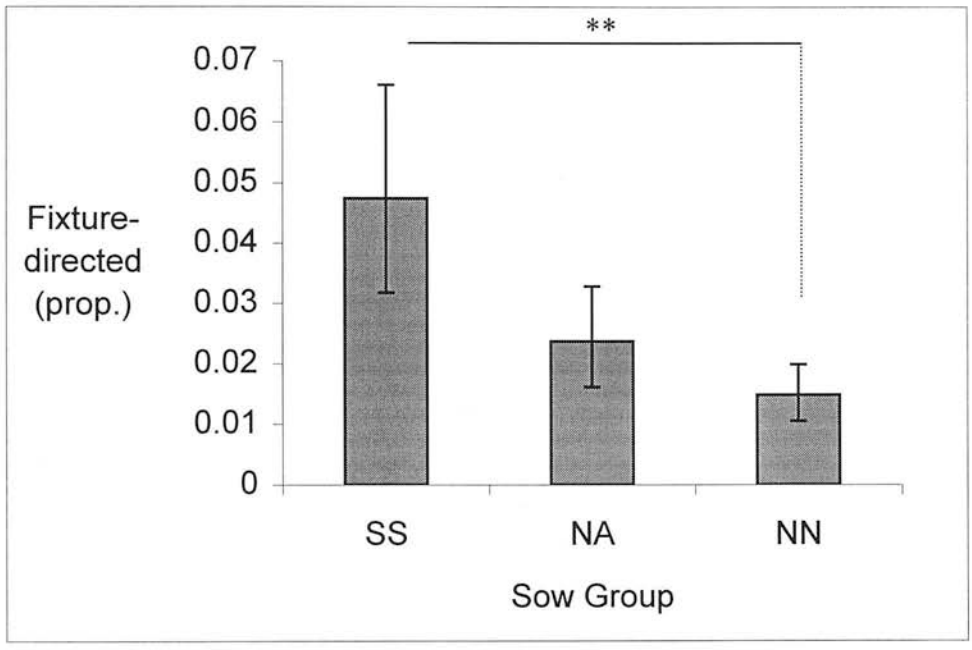


Figure 6.7: Proportion time spent in fixture-directed behaviour (+/- 95% confidence interval) between -4 and 0 hours pre-farrowing, for savaging (SS), non-savaging but aggressive (NA) and non-savaging, non-aggressive gilts (NN). Values are back-transformed REML estimates, adjusted for repeated measures and controlled for parity, breed, season, age of sow, whether straw was present, time of day, farrowing house, whether a radio was on in the farrowing house. ** = p<0.01



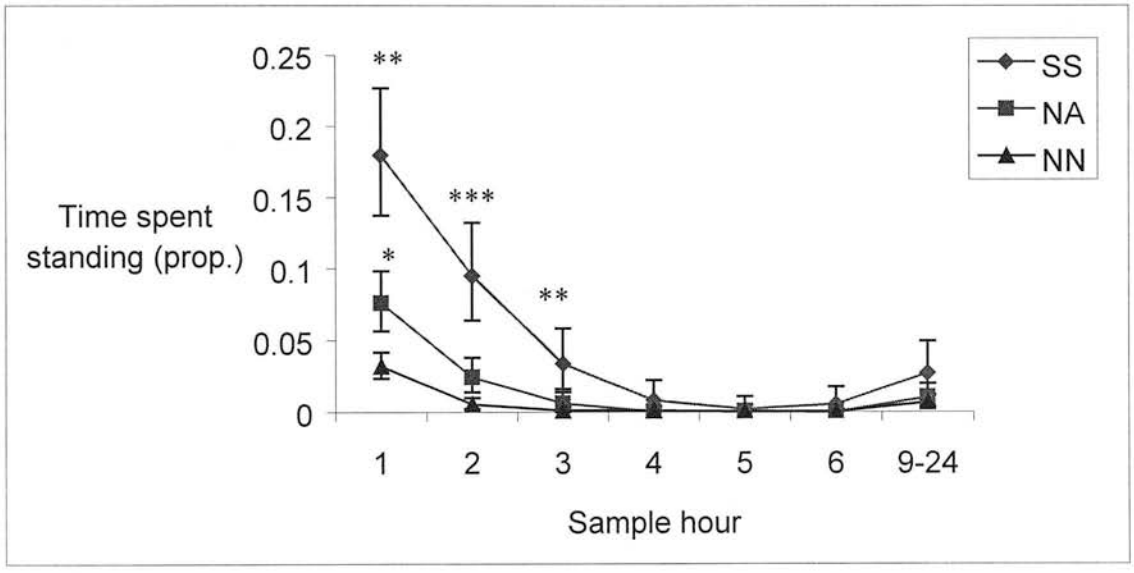
ii) Behaviour Following the Birth of the First Piglet (BFP)

In general behavioural differences between savaging and non-savaging sows were most noted during the first few hours following the onset of parturition (BFP). From approximately the fourth hour following BFP onwards, there were few behavioural differences between savaging and non-savaging sows.

During the first three hours following BFP, savaging gilts spent more time standing ($p<0.01$, $p<0.001$, $p<0.01$, respectively) than non-savaging non-aggressive sows and gilts (see figure 6.8). Non-savaging aggressive sows and gilts spent intermediate amounts of time standing that were significantly lower than savaging gilts during the first ($p<0.05$) and second hour ($p<0.05$) (see figure 6.8). After the third hour post-

BFP, there were no differences between the savaging groups in the time spent standing.

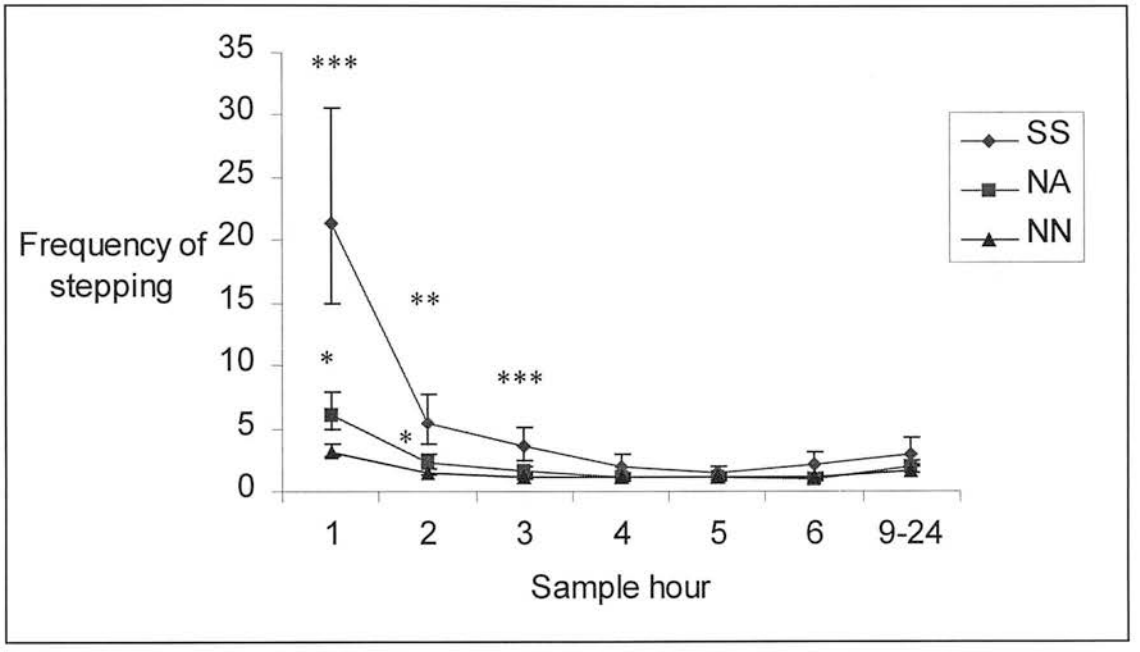
Figure 6.8: Mean time spent standing following the birth of the first piglet. The groups represented are savaging sows (SS), non-savaging but aggressive sows (NA) and non-savaging non-aggressive sows (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, litter size, age and season differences. Error bars show the 95% confidence intervals. See text for details. * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.



Savaging gilts also stepped more during the first three hours following BFP than non-savaging non-aggressive sows and gilts ($p<0.001$, $p<0.01$, $p<0.001$, respectively) (see figure 6.9). Non-savaging aggressive sows and gilts stepped an intermediate amount, significantly less than savaging gilts during the first ($p<0.05$) and second hour ($p<0.05$) (see figure 6.9). *

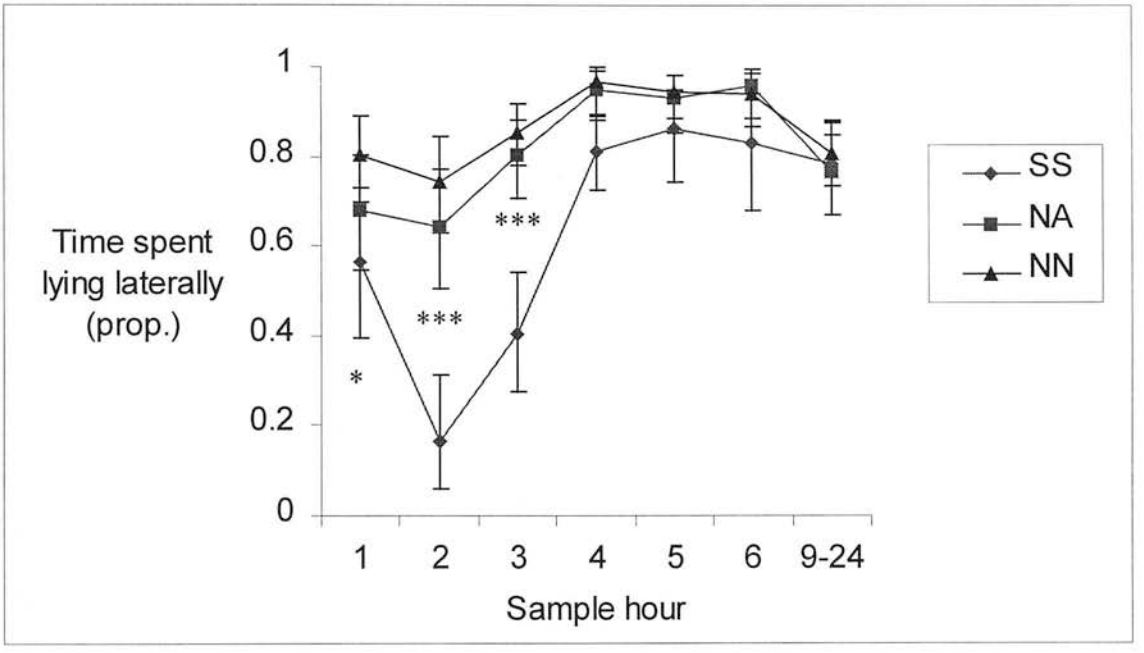
Figure 6.9: Mean frequency of stepping following the birth of the first piglet. The groups represented are savaging sows (SS), non-savaging but aggressive sows (NA) and non-savaging non-aggressive sows (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, litter size, age and season differences. Error bars show the 95% confidence intervals.

* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.



Also during the first three hours following BFP, savaging gilts spent less time lying laterally than non-savaging non-aggressive sows and gilts ($p<0.05$, $p<0.001$, $p<0.001$, respectively) (see figure 6.10). Non-savaging aggressive sows and gilts spent an intermediate amount of time lying laterally, that was significantly higher than savaging gilts during the second ($p<0.001$) and third hours ($p<0.001$) (see figure 6.10).

Figure 6.10: Mean proportion of time spent lying laterally (+/- 95% confidence interval) over successive sample hours during 24 hours following the onset of parturition. Data for three groups of sow are presented - savaging sows (SS), non-savaging but aggressive sows (NA), non-savaging, non-aggressive (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, age, litter size, season differences. See text for details. * = $p<0.05$, *** = $p<0.001$



During the first hour following BFP, savaging sows spent more time looking at piglets ($t_{116} = 2.3$, $p<0.05$) and made more glances towards piglets than non-savaging, non-aggressive sows ($t_{116} = 3.2$, $p<0.01$) (see Table 6.4). Non-savaging aggressive sows had intermediate values that were not significantly different to the other two groups of sow (see Table 6.4).

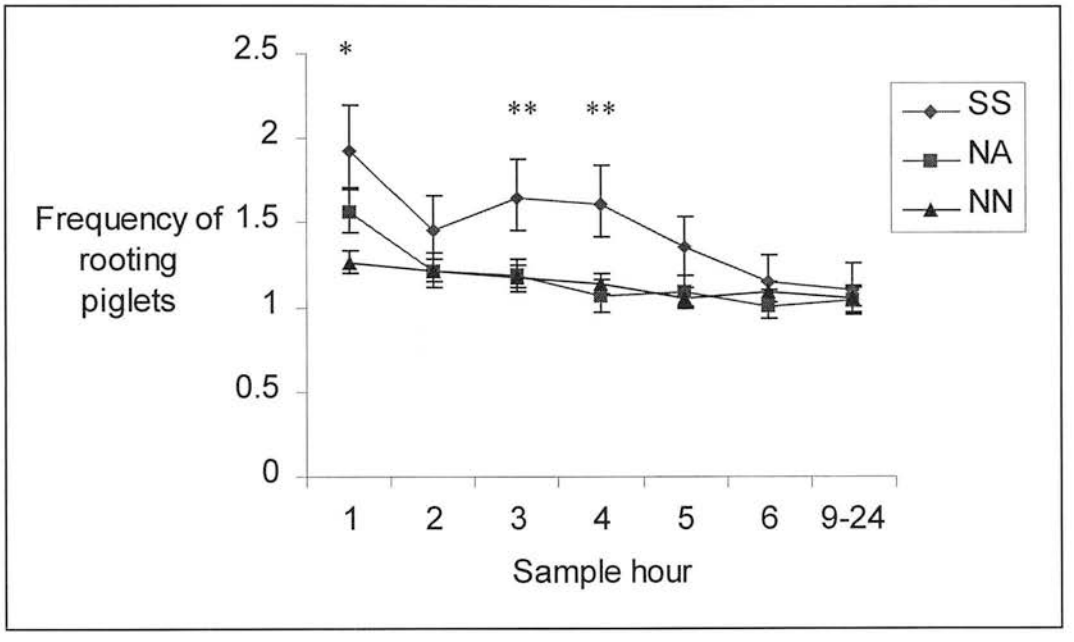
Table 6.4: Differences between savaging gilts (SS), non-savaging aggressive sows and gilts (NA) and non-savaging, non-aggressive sows in the time spent looking at piglets and the frequency of looking at piglets during the first hour following the onset of parturition. 95% confidence intervals are shown in brackets. Means with different superscripts differ significantly at $p<0.05$.

Behaviour	**Savaging group**		
	SS	**NA**	**NN**
Time spent looking at piglets	$2.5\%^{a}$ (1.5 - 3.8%)	$1.9\%^{ab}$ (1.5 - 2.5%)	$0.8\%^{b}$ (0.6 - 1.0%)
Frequency of looking at piglets	6.0^{a} (4.6 - 7.9)	3.5^{ab} (3.1 - 4.1)	2.7^{b} (2.5 - 2.9)

During the first ($p<0.05$), third ($p<0.01$) and fourth ($p<0.01$) hours following BFP, savaging gilts were observed pushing piglets away with their snout more than non-savaging, non-aggressive sows and gilts (see figure 6.11). Non-savaging but aggressive sows and gilts had intermediate values that were significantly lower than savaging gilts during the third ($p<0.05$) and fourth ($p<0.01$) hours (t_{50} = 2.5, 3.0, respectively) (see figure 6.11).

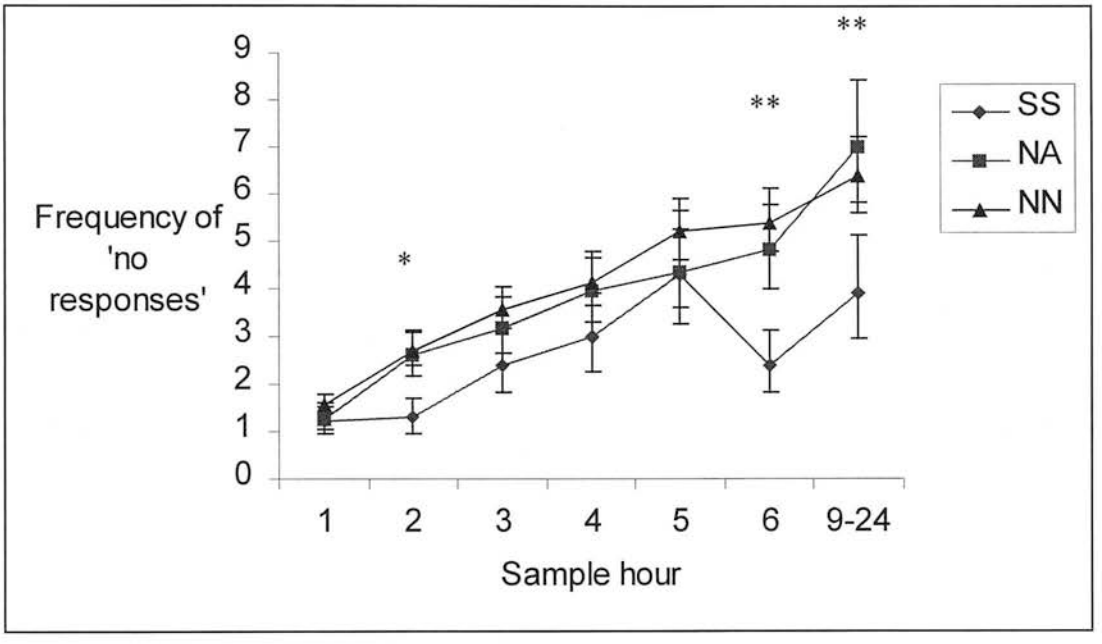
Figure 6.11: The mean frequency of pushing piglets away with the snout (rooting) over successive sample hours following the birth of the first piglet. The groups represented are savaging sows (SS), non-savaging but aggressive sows (NA) and non-savaging non-aggressive sows (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, age, litter size, season differences. Error bars show the 95% confidence intervals. See text for details.

* = $p<0.05$, ** = $p<0.01$



Savaging sows made fewer 'no responses' when a piglet approached the head during the second ($p<0.05$) and sixth hours ($p<0.01$) and during the samples made between 9 and 24 hours post-BFP ($p<0.05$) than non-savaging non-aggressive sows (t_{116} = 2.4, 2.8, 2.4, respectively) (see figure 6.12). Non-savaging aggressive sows made an intermediate number of 'no responses', significantly more than savaging sows during the sixth hour ($p<0.05$) and between 9 and 24 hours post-BFP ($p<0.01$) (t_{50} = 2.4, 2.7, respectively) (see figure 6.12).

Figure 6.12: The mean frequency of not responding to a piglet approaching a sows head (+/- 95% confidence intervals). The groups represented are savaging gilts (SS), non-savaging but aggressive sows and gilts (NA) and non-savaging non-aggressive sows and gilts (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, age, litter size, season, time of day, farrowing house, whether cross-fostering occurred and whether there was a radio on in the farrowing house. See text for details. * = $p<0.05$, ** = $p<0.01$



Savaging gilts made fewer nose to body contacts with piglets than non-savaging aggressive sows and gilts during the second hour post-BFP ($t_{50} = 2.2$, $p<0.05$) and fewer than non-savaging non-aggressive sows and gilts in the sixth hour post BFP ($t_{116} = 2.3$, $p<0.05$) (see Table 6.5).

Nose to nose sow-piglet contacts were seen less frequently amongst savaging gilts during the third hour post-BFP ($p<0.05$) and between 9-24 hours post-BFP ($p<0.05$) than non-savaging non-aggressive sows ($t_{116} = 2.3$, 2.2, respectively) (see Table 6.5).

Overall, savaging gilts were more responsive towards piglets during the first ($p<0.05$) and second hour ($p<0.01$) post-BFP than non-savaging non-aggressive sows and gilts ($t_{116} = 2.10$, 2.70, respectively) (see Table 6.5).

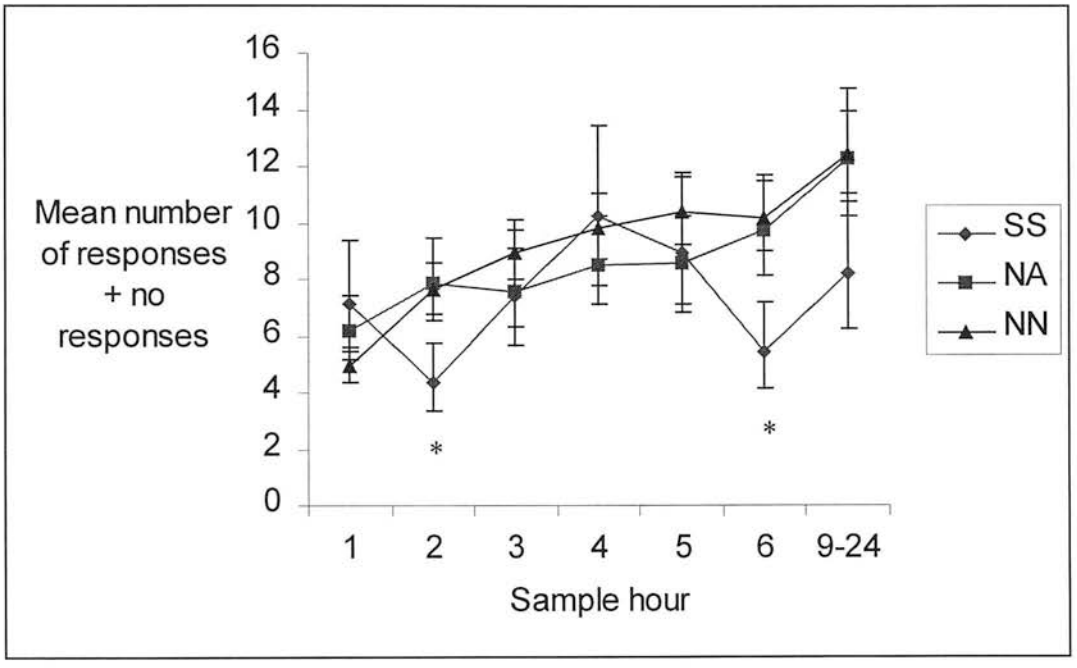
Table 6.5: Differences between the savaging groups in the frequency of nose to nose and nose to body sow-piglet contacts during the 24 hours following the onset of parturition. Means with different superscripts differed significantly at $p<0.05$.

Behaviour and time sample	Savaging group		
	SS	NA	NN
Nose-body (2nd hour)	2.1^{a} (1.6 - 2.7)	3.8^{b} (3.2 - 4.5)	3.4^{ab} (3.1 - 3.8)
Nose-body (6th hour)	1.7^{a} (1.3 - 2.2)	3.1^{ab} (2.6 - 3.7)	3.4^{b} (3.0 - 3.8)
Nose-nose (3rd hour)	2.2^{a} (1.7 - 2.8)	2.4^{ab} (2.0 - 2.8)	3.2^{b} (2.9 - 3.5)
Nose-nose (9-24 hours)	1.9^{a} (1.5 - 2.5)	2.4^{ab} (2.0 - 2.8)	3.0^{b} (2.7 - 3.4)
Responsiveness (1st hour)	0.95^{a} (0.77 - 1.00)	0.80^{ab} (0.71 - 0.90)	0.64^{b} (0.59 - 0.69)
Responsiveness (2nd hour)	0.86^{a} (0.68 - 1.00)	0.48^{ab} (0.39 - 0.58)	0.46^{b} (0.42 - 0.51)

There were no differences between the litters of savaging and non-savaging sows in time spent close to the sows head (measured using scan samples). When a piglet comes within one body-length of a sows head, the sow can either a) respond to the piglet (e.g. nose, touch, bite, snap or root), b) not respond to the piglet whereby the sows does not move, or c) re-coil away from the piglet. Re-coiling away from a piglet was not measured directly but can be inferred if a) and b) are known and given that there was no difference between the litters in the time spent near the sows head.

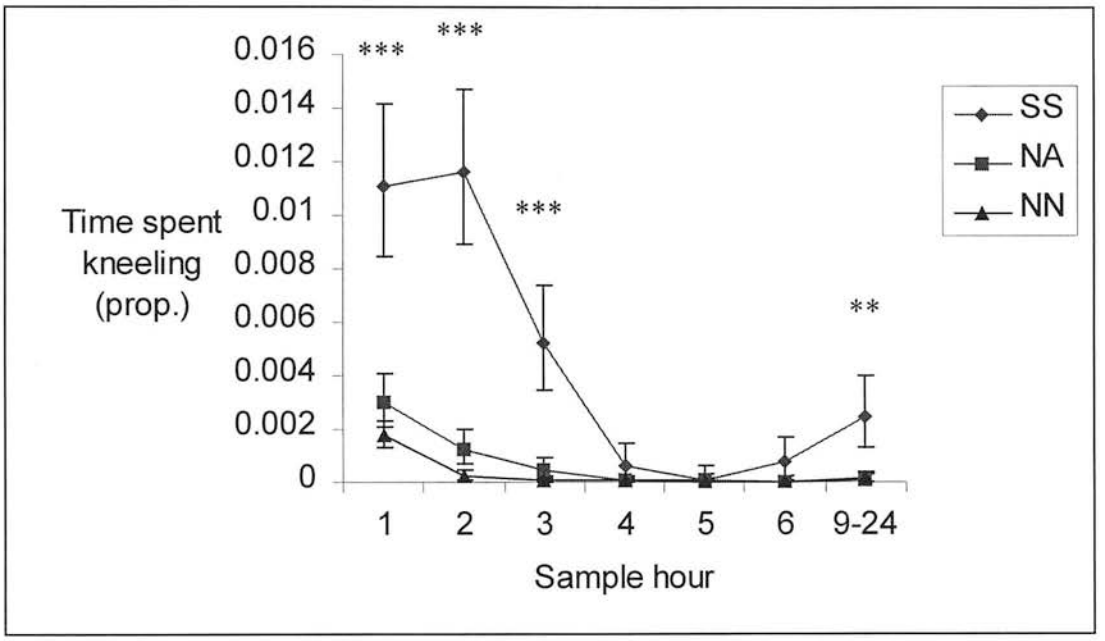
During the second ($p<0.05$) and sixth hours ($p<0.02$), the total number of no responses plus responses was lower in savaging gilts than non-savaging non-aggressive sows and gilts ($t_{116} = 2.3$, 2.6, respectively). On the basis of this result there is some evidence to suggest that savaging sows were more likely to re-coil away from piglets than non-savaging non-aggressive sows (see figure 6.13).

Figure 6.13: The mean total number of responses (nose, touch, root, bite, snap) plus the total number of no responses, per hour following the birth of the first piglet. The groups represented are savaging sows (SS), non-savaging but aggressive sows (NA) and non-savaging non-aggressive sows (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, age, litter size, season, time of day, farrowing house, whether cross-fostering occurred and whether there was a radio on in the farrowing house. Error bars show the 95% confidence intervals. See text for details.
* = $p<0.05$



During the first ($p<0.001$), second ($p<0.001$), third hours ($p<0.001$) and between 9-24 hours ($p<0.01$) following BFP, savaging gilts spent more time kneeling than non-savaging non-aggressive sows and gilts (t_{116} = 5.3, 4.5, 5.9, 3.2, respectively). Similarly, during the same observation hours (same levels of significance), savaging gilts spent more time kneeling than non-savaging aggressive sows and gilts (t_{50} = 3.5, 5.0, 3.5, 2.7, respectively) (see figure 6.14).

Figure 6.14: Mean time spent kneeling (+/- 95% confidence intervals) following the birth of the first piglet. The groups represented are savaging sows (SS), non-savaging but aggressive sows (NA) and non-savaging non-aggressive sows (NN). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, age, litter size, season, time of day, farrowing house, whether cross-fostering occurred and whether there was a radio on in the farrowing house. See text for details. ** = $p<0.01$, *** = $p<0.001$



During the second ($p<0.05$) and third hour ($p<0.02$) following BFP, savaging gilts spent more time interacting with the straw or floor of the than non-savaging non-aggressive sows and gilts ($t_{116} = 2.2, 2.5$, respectively) (see Table 6.6).

Table 6.6: Behavioural differences between savaging gilts (SS), non-savaging aggressive sows and gilts (NA) and non-savaging non-aggressive sows and gilts (NN). Means with different superscripts differ significantly at $p<0.05$.

Behaviour and time sample	**Savaging group**		
	SS	**NA**	**NN**
% Straw/floor-directed (2^{nd} hour)	$3.2\%^{a}$ (1.9 - 4.8%)	$1.5\%^{ab}$ (0.9 - 2.2%)	$0.5\%^{b}$ (0.2 - 0.8%)
% Straw/floor-directed (3^{rd} hour)	$1.6\%^{a}$ (0.7 - 2.8%)	$0.6\%^{ab}$ (0.2 - 1.1%)	$0.2\%^{b}$ (0.0 - 0.3%)
Push against back of crate (frequency, 3^{rd} hour)	1.3^{a} (1.1 - 1.5)	1.1^{ab} (1.0 - 1.2)	1.0^{b} (0.9 - 1.1)
Near-miss (frequency, 3^{rd} hour)	1.4^{a} (1.3 - 1.6)	1.0^{b} (0.9 - 1.2)	1.1^{b} (1.0 - 1.2)

In the third hour, savaging gilts made more attempts to back out of the crate than non-savaging non-aggressive sows and gilts ($t_{116} = 2.5$, $p<0.02$) (see Table 6.6). Also in the third hour, savaging gilts had more 'near miss' events (almost crushing a piglet) than non-savaging aggressive ($t_{50} = 3.0$, $p<0.01$) or non-savaging non-aggressive sows and gilts ($t_{116} = 3.1$, $p<0.01$) (see Table 6.6).

The behaviour and location of the litters of savaging and non-savaging sows and gilts also differed during certain time samples. These savaging group differences are summarised in Table 6.7 and in figure 6.15.

Table 6.7: Differences between the litters of savaging gilts (SS), non-savaging aggressive sows and gilts (NA) and non-savaging non-aggressive sows and gilts (NN), in their behaviour and location. Means with different superscripts differed significantly at $p<0.05$ (t-distribution).

Behaviour and time sample	Savaging group		
	SS	NA	NN
% creep (2nd hour)	4.0%[a] (2.0 - 6.8%)	0.9%[b] (0.3 - 1.8%)	0.4%[b] (0.1 - 0.8)
% creep (3rd hour)	3.2%[a] (1.4 - 5.7%)	1.5%[ab] (0.7 - 2.6%)	0.7%[b] (0.3 - 1.2%)
% creep (4th hour)	11.2%[a] (7.6 - 15.4%)	2.3%[b] (1.3 - 3.6%)	1.4%[b] (0.9 - 2.1)
% creep (5th hour)	7.6%[a] (4.7 - 11.2%)	4.0%[ab] (2.6 - 5.7%)	1.8%[b] (1.2 - 2.6%)
% udder active (2nd hour)	17.0%[a] (11.6 – 23.2%)	42.1%[b] (37.3 – 47.0%)	49.4%[b] (46.2 – 52.6%)
% udder active (3rd hour)	36.9%[a] (29.7 – 44.5%)	51.6%[ab] (46.7 – 56.5%)	54.0%[b] (50.8 – 57.2%)
% udder inactive (2nd hour)	0.9%[a] (0.1 – 2.4%)	4.4%[b] (2.9 – 6.1%)	3.4%[b] (2.6 – 4.4%)

During the second ($p<0.01$), third ($p<0.02$), fourth ($p<0.001$) and fifth hour ($p<0.01$) following BFP, the litters of savaging gilts spent more time in the creep than the litters of non-savaging sows and gilts ($t_{116} = 3.0, 2.5, 4.1, 2.7$, respectively) (see Table 6.7). The litters of non-savaging aggressive sows and gilts spent similar amounts of time in the creep as non-savaging non-aggressive sows and gilts. The litters of savaging gilts spent significantly more time in the creep than non-savaging aggressive sows and gilts during the second ($t_{50} = 2.1$, $p<0.05$) and fourth hour following BFP ($t_{50} = 3.2$, $p<0.01$) (see Table 6.7).

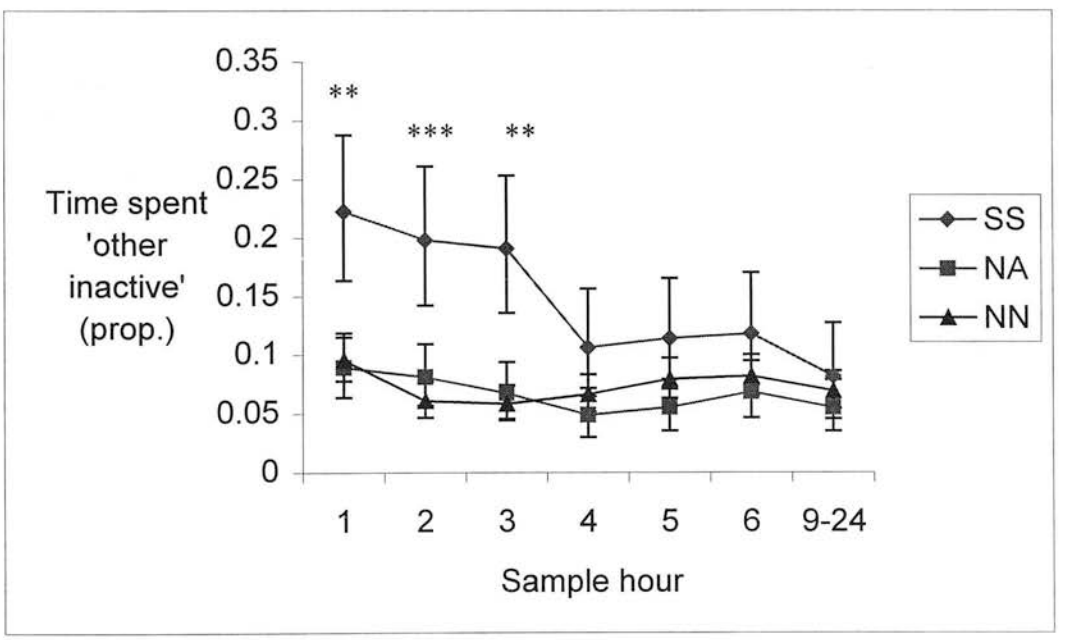
The litters of savaging gilts spent less time active at the udder than the litters of non-savaging non-aggressive sows and gilts during the second ($p<0.001$) and third hour ($p<0.05$) following BFP ($t_{116} = 3.5, 2.6$, respectively). The litters of savaging sows

also spent less time active at the udder than non-savaging aggressive sows during the second hour (42.1%, 95% CI = 37.3 - 47.0%; $t_{50} = 2.4$, $p<0.05$) (see Table 6.7).

In addition, during the second hour following BFP, the litters of savaging sows spent less time inactive at the udder than the litters of non-savaging aggressive ($t_{50} = 2.1$, $p<0.05$) and non-savaging non-aggressive sows and gilts ($t_{116} = 2.4$, $p<0.05$) (see Table 6.7).

During the first ($p<0.01$), second ($p<0.001$) and third ($p<0.01$) hours following BFP, the litters of savaging gilts spent more time inactive and away from the sow or creep ('other inactive') than non-savaging non-aggressive sows and gilts ($t_{116} = 2.9, 3.4, 3.3$, respectively) (see figure 6.15).

Figure 6.15: The proportion of the litter inactive and away sow or creep per hour (12 scans) (+/- 95% confidence intervals). The litters of savaging gilts (SS), non-savaging aggressive sows and gilts (NA) and non-savaging non-aggressive sows and gilts (NN) are represented. Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, age, litter size, season, time of day, farrowing house, whether cross-fostering occurred and whether there was a radio on in the farrowing house. See text for details. ** = $p<0.01$, *** = $p<0.001$



Correlations between different piglet-directed behaviours

The relationships between the five sow-piglet interactions - bite, snap, root, touch and nose - were explored using Pearson product moment correlations.

Snap	**0.655**			
Root	**0.309**	0.245		
Touch	-0.123	-0.099	**0.589**	
Nose	**-0.309**	**-0.367**	0.182	**0.502**
	Bite	Snap	Root	Touch

Biting was positively correlated to snapping ($p<0.001$) and rooting piglets ($p<0.01$) and negatively correlated to nose to nose contacts ($p<0.01$). Nose to nose contacts were positively correlated to nose to body contacts ($p<0.001$) and negatively correlated to snapping ($p<0.01$). Root was positively correlated to nose to body contacts ($p<0.001$).

Lack of Consistency in Piglet-directed Aggression Over Two Parities

From the 11 savaging gilts observed, 5 were not culled and were observed again in parity two. Only two of these five sows performed any sort of piglet-directed aggression in parity two (two attempted bites from both sows). There were 17 parity one non-savaging aggressive gilts (NA) with repeated measures over two parities. Of these only three showed any form of aggression in parity 2, out of a total of 12 parity two aggressive but non-savaging sows.

The percentage of parity two sows showing piglet-directed aggression was 21%. This is similar to the percentage of aggressive parity one gilts (23%, savaging or non-savaging) that showed piglet-directed aggression in parity two. Therefore, piglet-directed aggression would appear to be a random occurrence.

Discussion

The adaptive brood reduction hypothesis of savaging predicts that savaging should be more common amongst larger litters and brood reduction should be focussed on the weaker offspring. Savaging was not effected by litter size and the onset of piglet-directed aggression from savaging gilts always occurred before the end of parturition. Piglets born towards the end of parturition tend to be weaker than those born at the start of parturition (Dawes *et al.*, 1963; Randall, 1971; English and Wilkinson, 1982). Therefore, the occurrence of savaging in this sample of sows and gilts does not appear to have a adaptive brood-reducing function.

In the light of no alternative functional hypothesis, the possibility that savaging is a non-adaptive behaviour should be considered. Piglet savaging behaviour in commercial gilts could be a response to some aspect of the captive environment. It is possible that a random mutations in the genes, that build up over generations, might have produced a genotype that is predisposed to savage under certain environmental conditions. The absence of natural selection acting on commercially reared pigs may have resulted in these genotypes increasing in the population. However, it is not known how the incidence of non-adaptive piglet savaging in commercial pigs compares to the incidence of non-adaptive piglet savaging in wild pigs.

Savaging occurred too infrequently to determine whether the incidence of this mortality was influenced by breed (see Chapter 5). However, previous research has indicated that piglet savaging is a heritable trait (Knap and Merks, 1987; van der Steen *et al.*, 1988). The occurrence of piglet-directed aggression did not appear to be consistent within sows over parities one and two but confounding factors between the parities (e.g. season) may have influenced this result. Savaging only occurred in parity one, despite five savaging gilts also farrowing in parity two. This suggests that an environmental factor only present during parity one interacts with the genotype predisposed for savaging, resulting in the incidence of savaging observed. In reality, there may be more than one parity one dependent environmental factor that induces piglet savaging.

The nest-building behaviour savaging gilts was different to that of non-savaging sows and gilts. At a time when most sows and gilts were increasing the amount of time spent engaged in straw or floor-directed behaviour (-16 to -12 hours), savaging gilts did hardly any. If savaging sows were spending more time inactive instead of engaged in straw and floor-directed behaviour, one might conclude that savaging sows were less motivated to nest-build. However, savaging sows were just as active as non-savaging sows but spent more time laying ventrally and changed lying postures more frequently than non-savaging sows and gilts. This restlessness indicates frustration of nest-building motivation. The inability to adapt nest-building behaviour to the confined environment of the farrowing crate may be one of the factors that induces piglet savaging behaviour.

The crate-induced nest-building frustration, apparent between -16 and -12 hours, was short-lived since between -10 and -6 hours pre-farrowing, there were no behavioural differences in the time budgets of savaging and non-savaging sows. It is likely that a comparison of time budgets is not sensitive enough to detect all the potential differences between the nesting behaviour of savaging and non-savaging sows. A sequence analysis such as that performed by Horvath (1996) on nest-building behaviour might detect important differences here. During the period prior to the onset of parturition, savaging sows were observed mouthing the crate bars and fixtures more than non-savaging sows. This behaviour may either reflect some re-directed nest-building motivation or frustration at being confined (Jensen, 1993; Hartsock and Baczewski, 1997). In Chapter 3, data is presented suggesting that some fixture-directed behaviour is governed by escape motivation. Higher levels of fixture-directed behaviour prior to parturition was common to savaging sows regardless of whether they had straw or not, suggesting that this behaviour is an expression of frustration at being confined rather than nest-building motivation (Hartsock and Baczewski, 1997).

Pre-farrowing nesting behaviour appears to be partly governed by hormonal factors (Jensen, 1993; Boulton *et al.*, 1997a; Gilbert and Burne, 2000). And we know that parturition is associated with major hormonal changes that can radically change how mothers respond to young (Pederson *et al.*, 1982; Elwood and Ostermeyer, 1984; Poindron *et al.*, 1984; Lawrence *et al.*, 1997). Feedback from the performance of

nesting will influence the hormonal state of the sow, so if this feedback is not forthcoming, the hormonal changes necessary for maternity could be disrupted. Such that when piglets arrive, some sows may not be hormonally-primed to respond to their piglets in an appropriate way. This may explain why savaging sows spend more time engaged in straw and floor-directed behaviour after parturition starts.

If the fulfilment of nest-building motivation is important in preparing a sow or gilt for maternity then a greater number of savagings might have been expected in the absence of straw. The low incidence of savaging and large number of potentially confounding factors between litters makes it impossible to assess whether a straw effect existed. However, savaging did not appear to be more frequent in the absence of straw. This is contrary to what Sambraus (1976) and Brummer (1972) reported (cited in Fraser and Broom, 1990) but supports the findings of Hansen and Curtis (1981). In Chapter 3, data is presented showing that straw promotes the expression of nest-building behaviour, a finding that is supported by the majority of the background literature (Cronin and Van Amerongen, 1991; Arey, 1992; Jensen, 1993; Cronin *et al.*, 1993; Burne *et al.*, 2000). However, it is possible that straw is not such an important modifier of pre-farrowing behaviour as we previously thought, since for savaging gilts it does not appear to promote the adaptation of nest-building behaviour to the farrowing crate. The rooting movements of sows during nest-building in the crate quickly causes the straw to be pushed out of reach. When this happens straw is likely to be still visible to the sow, influencing her motivation to nest (Jensen, 1993; Cronin *et al.*, 1994), but inaccessible leading to increased thwarting of nest-building motivation.

Once parturition starts, there was a tendency for savaging gilts to have a faster rate of parturition prior to the onset of aggression than non-savaging gilts of the same breed, farrowing at the same time of year and with similar litter sizes. The lack of a clear difference here does not support the hypothesis that savaging gilts have higher levels of oxytocin at parturition due to inefficient opioid inhibition of the oxytocin system caused by chronically high opioid tone prior to parturition. However, this hypothesis cannot be falsified on the basis of this result alone. Falsification of this hypothesis would require direct physiological measurements of circulating oxytocin and of the levels of opioids required to inhibit oxytocin release.

The number of piglets born from savaging gilts was higher prior to the first nose-nose contact than that for non-savaging sows or gilts. Nose to nose contacts between the sow or gilt and her piglets are thought to necessary for successful mother-offspring bonding (Grundlach, 1968; Whatson and Bertram, 1983; Jensen and Redbo, 1987). Thus, delayed mother-offspring bonding, relative to the progress of parturition, would appear to be an important factor in the aetiology of savaging.

The onset of piglet-directed aggression amongst savaging gilts was associated with a slowing of the rate of piglet expulsion. This result, not previously reported in the literature, suggests suppression of the process that results in piglet expulsion, i.e. oxytocin acting on the smooth muscle of the uterus. Opioids are known to inhibit the release of oxytocin (Douglas *et al.*, 1993, 1995; Onaka *et al.*, 1995; Lawrence *et al.*, 1997) and opioids are released in response to aversive environmental stimuli (Amir *et al.*, 1980; Laatikainen, 1991; Lawrence *et al.*, 1997). Therefore, piglet-directed aggression may associated with an aversive psychological state in the gilt.

The behaviour of the savaging gilt also suggests an aversive psychological state. Savaging gilts were generally more restless than non-savaging sows and gilts, changing postures frequently, stepping frequently and pushing against the back bar of the crate more frequently. Many of these behavioural differences are consistent with what others have found (e.g. Ahlstrom, 1997; Calvert, 1997). Most behavioural differences were confined to the first few hours following the onset of parturition, which also marks the period when savaging occurred. However, savaging gilts continued to make fewer 'no responses' during the sixth hour and between 9 and 24 hours following the onset of parturition. There is also some evidence to suggest that savaging gilts are more likely to re-coil away from piglets when they approach, even after piglet-directed aggression has begun, than non-savaging gilts and sows. These results suggest that savaging gilts are more nervous of their piglets than non-savaging sows and gilts.

Savaging sows differed from non-savaging sows in the type of piglet-directed responses they made. Savaging gilts made fewer nose to body and nose to nose responses than non-savaging sows and gilts, whilst making more snap and bite

responses. In addition, biting and snapping at piglets correlated negatively with nose to nose ('nose') and nose to body ('touch') sow-piglet contacts. These findings suggest that inappropriate bite and snap responses and being made in place of the normal sow-piglet bonding behaviours, indicating that savaging gilts may not know how to act towards piglets. Overall, savaging gilts were more responsive to their piglets during the first two hours following the onset of parturition, but clearly those responses were due to aggressive interaction rather than interactions related to sow-piglet bonding

Rooting movements towards piglets correlated positively with biting but also nose to body contacts. These rooting movements were more common amongst savaging sows than amongst non-savaging sows, suggesting that rooting of piglets might be more of a negative interaction than a positive one. The distinction between rooting and touching piglets was not made in Ahlstroms (1997) study but it would appear from these results that this is a biologically relevant distinction to make.

In most cases the behavioural measures from aggressive but non-savaging sows and gilts were intermediate between measures from savaging sows and measures from non-savaging, non-aggressive sows and gilts. This suggests that degree of aggressiveness correlates with some behavioural measures, so it might be possible to assess risk of savaging by measuring deviations away from a behavioural optimum.

The litters of savaging and non-savaging gilts and sows also differed in their behaviour and location in the crate. Piglets of savaging gilts were more likely to be found in the creep than the piglets on non-savaging sows and gilts. This result is probably connected to the practice of shutting piglets in the creep when a sow or gilt is recognised as being aggressive towards her piglets. Although behavioural observations were not recorded during such human interventions, piglets with enforced experience of the creep will probably more readily enter the creep of the own accord once they are able to move freely. As with the sows behaviour, the behaviour and location of the litters of savaging and non-savaging sows differed most during the first few hours following the onset of parturition. During this time the litters of savaging gilts spend less time active at the udder (teat massage and jostling for position) and more time inactive away from the sow and creep than the litters of non-savaging sows. These differences are a consequence of savaging gilts spending

more time standing and kneeling and less time lying laterally than non-savaging sows and gilts. Interestingly, piglets did not seem to react to the risk posed by an aggressive sow or gilt by spending less time at the sows head. This indicates that either the piglets are incapable of assessing risk of aggression from the sow, or the benefits of being at the sows head outweigh the cost of possible aggression from the sow.

There was an indication that piglet-directed aggression might be more common amongst young for parity Duroc gilts. This result is consistent with the results of a recent study that found that Large White-Landrace sows, whose first farrowing was when they were less than a year old, weaned fewer piglets "especially at parity one" and so were less productive overall (Le Cozler *et al.*, 1998). Similarly, Legault *et al.* (1996) also found poor performance in the first parity from gilts whose first service was very early (5 months). However, contrary to Le Cozler *et al.* (1998), Legault *et al.* (1996) found that early servicing resulted in improved lifetime productivity of the sow. The poor performance of young for parity gilts may be connected to the tendency found here for a higher level of aggression amongst the young for parity Duroc gilts. Further research is needed to confirm this finding because, if confirmed, it offers farmers an easy way to reduce the incidence of piglet-directed aggression in the herd.

Sambraus (1976, 1985) suggested three types of savaging sow, which I describe in the introduction. No savaging sow in this study killed her entire litter. However, human intervention and sedation of the savaging gilt with drugs such as "Stresnil" for four of the eleven savaging gilts, may account for this. One gilt was reported to have bitten most of her litter, fitting in with Sambraus' third category of savaging - the sow that is overtly aggressive to both humans and her own piglets. In four cases, a savaging gilt also crushed a piglet, representing a marginally higher incidence of crushing amongst savaging gilts than in the population as a whole. Therefore some of the savaging gilts in this study may have been included in Sambraus' first category - savaging that follows accidental crushing. The majority of savaging gilts in this study seem to best fit Sambraus' second category of savaging - nervous sows that actively avoid their piglets and are aggressive only when they come too close. Evidence for this comes from the behaviour of savaging gilts after parturition has begun (see above).

This research has shown that piglet-savaging behaviour does not represent an adaptive brood reduction strategy. If savaging is not adaptive, then it must be maladaptive. In which case research needs to focus on identifying causal factors connected to the sows environment that promote savaging. In this study I have identified several factors associated with savaging, which further research may prove to have a causal role in the aetiology of savaging. These factors include the disruption of nest-building, delayed mother-offspring bonding, gilt nervousness, the novelty of the piglet stimulus and sow immaturity.

Summary and Conclusions

1. There was no effect of litter size on the occurrence of savaging and piglet-directed aggression begins before parturition finishes. This indicates that savaging behaviour does not appear to be an adaptive brood reduction mechanism to adjust litter size to a level that the sow perceives the environment can support.
2. Piglet-directed aggression was not consistently expressed by the same sows over parities one and two. Since we know that savaging is heritable (Knap and Merks, 1987; Van der Steen *et al.*, 1988), this result suggests that parity one specific environmental factors must be interacting with the genotype of gilt pre-disposed to savage.
3. There was a tendency for young Duroc gilts to exhibit more piglet-directed aggression than older Duroc gilts, indicating a possible effect of gilt maturity on piglet-directed aggression.
4. Savaging was associated with a disruption of nest-building during the 24 hours prior to parturition, indicating that savaging gilts are less able to adapt their nest-building behaviour to the farrowing crate than non-savaging sows and gilts. The presence of straw in the crate did not appear to influence the incidence of savaging. This suggests that straw does not promote the adaptation of nest-building behaviour to the crate in the sub-set of gilts that go on to savage.
5. In savaging gilts, Mother-offspring bonding is delayed relative to the progress of parturition. Thus, at the point in time when nose to nose contacts are seen, more piglets have been born in the litters of savaging gilts than non-savaging gilts.
6. The onset of piglet-directed aggression in savaging gilts was associated with a slowing in the rate of piglet expulsion, indicating inhibition of oxytocin induced uterine muscle contraction. This may be mediated through raised opioid tone, indicating that piglet-directed aggression may be associated with an aversive psychological state in the gilt.
7. The behaviour of savaging gilts following the onset of parturition suggests that these gilts are initially nervous of their piglets. After approximately three hours following the birth of the first piglet, there are few behavioural differences between savaging and non-savaging gilts that can be identified from time budget

data. This suggests that the factors that induce savaging in a small sub-set of gilts have only a transitory influence on gilt behaviour.

8. Differences in the behaviour of savaging and non-savaging sows and gilts are reflected in the behaviour and location of their litters. However, piglets do not respond to the risk posed by a savaging or aggressive sow or gilt by spending less time at the sow or gilts head. This suggests that either piglets are unable to assess this risk or the benefits of approaching the sows head outweigh the risk.

CHAPTER 7:

THE BEHAVIOURAL CHARACTERISTICS OF CRUSHING SOWS

Introduction

Crushing is the major cause of pre-weaning mortality in commercial pig production (Baxter, 1971; Glastonbury, 1977; Bolet, 1982; Spicer *et al.*, 1986; Svendsen *et al.*, 1986; Weary *et al.*, 1998; see also Chapter 5, this thesis). Modifications to the farrowing environment, such as low level bars to control how the sow moves, can reduce crushing mortalities (Green, 1981; Weary *et al.*, 1998). One of the aims of introducing farrowing crates into pig production systems was to reduce the number of piglet crushing mortalities (English and Edwards, 1996), which the majority of studies indicate that they do (e.g. Devilat *et al.*, 1971; Aherne, 1982; Collins *et al.*, 1987). Farrowing crates limit the number of crushing mortalities by reducing the speed and frequency with which posture changes are performed, e.g. lying down from a standing position (Baxter, 1984; p. 455) and rolling into a side lying posture (Weary *et al.*, 1996a). However, crushing remains the most prevalent cause of pre-weaning mortality when farrowing crates are used (Glastonbury, 1977; Friendship *et al.*, 1986; Spicer *et al.*, 1986; see also Chapter 5). In addition, some studies have found no difference between farrowing pen and farrowing crate systems in the incidence of crushing mortalities (Gustafsson, 1983; Collins *et al.*, 1987; Arey and Sancha, 1996). This suggests that a different strategy, other than limiting the movements of the sow, should be employed in order to reduce the number of piglet crushing mortalities.

The continuing problem of piglet crushing in modern pig production has resulted in some interesting theories as to why selective breeding can not seem to make much impact on the crushing statistics. Fraser (1990) has suggested that the high incidence of crushing is due to an evolved strategy "to over-produce young of heterogenous size and allow sibling competition to do any necessary culling". Wechsler and Heggin (1997), on the other hand, argue that the high incidence of crushing is a consequence

of high litter sizes and the breeding of large docile sows that are careless when lying down. Frasers' (1990) hypothesis is an interesting way of considering the problem of piglet crushing, suggesting that a mechanism employed by Wild Boar to ensure the survival of the fittest piglets remains in the commercial genotype, unaffected by the domestication process. Whereas, Wechsler and Hegglins' (1997) hypothesis is more an indictment of the uncoupling of reproductive success from maternal rearing ability through the action of artificial selection.

Sibling competition has long been recognised as a contributory factor in piglet mortality (English and Smith, 1975; Hartsock and Graves, 1976). That sibling competition might be an adaptive strategy would explain why piglets are born with such sharp teeth that seem ideal for the sideways biting movements employed during teat disputes (Fraser, 1975, 1990). The over-production of young is a strategy employed by many animals (e.g. see Mock, 1984, for a review of bird examples). Such a strategy is adaptive because the additional investment of producing extra young is small compared to lactation costs (Clutton-Brock *et al.*, 1989), whilst the benefit of having the flexibility to rear an extra offspring, should conditions improve, is great.

Piglets that fail to compete successfully for teats have an increased risk of crushing not only from being too weak to avoid a posture-changing sow (English and Morrison, 1984) but also from spending more time close to the udder (Weary *et al.*, 1996b). Uncompetitive piglets, as identified from their poor weight gains, must trade-off risk of starvation with risk of crushing (Weary *et al.*, 1996b). Remaining attached to a teat and massaging the udder between sucklings brings with it potential benefits in terms of improved resource defence (Leimar and Enquist, 1984) and increased milk production (Algers and Jensen, 1985, 1991). Thus, crushing and starvation are intimately linked, with sibling competition influencing both (English and Smith, 1975; Fraser, 1990).

Frasers' (1990) hypothesis of crushing being the result of an adaptive mechanism primarily governed by sibling competition places little emphasis on the influence of the sows behaviour on crushing mortalities. However, several studies have found that individual differences in sow behaviour can influence the incidence of crushing

(Edwards *et al.*, 1986; Olsson and Svendsen, 1989; Weary *et al.*, 1996a; Wechsler and Hegglin, 1997; Marchant *et al.*, 1996, 1997). Many of these studies have focussed on what types of posture change result in piglet crushing, which seems to be dependent on the accommodation type (Olsson and Svendsen, 1989; Weary *et al.*, 1996a). In farrowing crates, lying down from either a standing or sitting posture results in the most piglet crushings (Edwards *et al.*, 1986), whilst stepping on piglets (Olsson and Svendsen, 1989) and moving from a lying to a sitting posture (Weary *et al.*, 1996a) can also result in piglet crushings. In open farrowing systems Marchant *et al.*, (1997) found that stand to lie posture changes and swapping sides whilst lying are among the more dangerous posture changes a sow can make. It would also appear that sows in open farrowing systems can limit how dangerous their lying down can be by combining lying down quickly with being attentive to where the piglets are before lying down (Marchant *et al.*, 1996). However, this strategy does not always work and can depend on how eager the piglets are to suckle (Dr. J. N. Marchant, pers. comm.). Wechsler and Hegglin (1997) used a combination of behavioural measures related to frequencies of lying down and rolling onto the side whilst lying, along with measures of whether piglets were present in the lying area to produce a score that predicted risk of crushing.

As well as being aware of where piglets are prior to lying and avoiding dangerous posture changes, a sow might be able to reduce the risk of crushing by being alert to the alarm calls of her piglets. The playback of a piglet scream causes sows to respond by changing posture, looking at the speaker or increasing the time taken to lie, whilst visual and tactile piglet cues have no such effect (Hutson *et al.*, 1991; Hutson *et al.*, 1993). The higher the volume of the piglet call, the more responsive the sow is (Hutson *et al.*, 1993), suggesting that this is an honest signal of piglet need. Individual variation in the response of sows to a piglet alarm call is large, with only approximately 60% of sows responding to calls (Hutson *et al.*, 1991; Cronin and Cropley, 1991). This has led to speculation that there might be genetic variation in this trait that could be utilised in selection programmes (e.g. Hutson *et al.*, 1991). Wechsler and Hegglin (1997) later found that the individual variation in the responsiveness of sows was correlated to the percentage of crushing deaths. This finding renewed interest in the piglet squeal test as a measure of maternal quality for use in selection programmes (e.g. Rhydmer *et al.*, 1998; Thodberg *et al.*, 1998;

Grandinson *et al.*, 2000). Unfortunately the correlation Wechsler and Hegglin (1997) found has yet to be repeated and the sows response to a piglet squeal appears to lack much individual consistency over subsequent parities (Rhydmer *et al.*, 2000). This casts doubt on the suitability of using the piglet scream test as a measure of risk of crushing.

The present study was designed to look at general behavioural characteristics of sows that crush their piglets, the starting point being the piglet mortalities and relating these to sow behaviour, rather than vice versa as in the Wechsler and Hegglin (1997) study. The relationships between different types of posture change and the occurrence of crush or near-crush events were explored for comparison with the Edwards *et al.* (1986), Olsson and Svendsen (1989) and Weary *et al.* (1996a) studies. I was also interested to see if any of the behavioural predictors of crushing in open pen systems identified by Marchant *et al.* (1996, 1997) and Wechsler and Hegglin (1997) held true for sows in the crate system.

Methods

Experimental Design

The experiment was based around a breed by parity by treatment factorial design whereby individual sows were observed over two parities. The design was unbalanced largely as a result of sows 'dropping out' between parities (see chapter 2). Treatment was the presence or absence of straw that was allocated randomly within breeds (see chapter 2).

Observations were made from 96 parity one gilt farrowings and 63 parity two sow farrowings. In 57 cases the same individual was observed over both parities.

Behavioural Observations

Sows and gilts were observed during 10-minute samples at -24, -20, -16 hours and then every two hours until the birth of the first piglet (BFP) (see Chapter 2). Following BFP, each sow and gilt was observed for six hours continuously and then for a further six 10-minute samples at 9, 12, 15, 18, 21 and 24 hours. The pre-farrowing behaviour of sows and gilts was summarised as four time blocks: -24, -20 hours; -16 to -12 hours; -10 to -6 hours; -4 to 0 hours. The behavioural time budget of sows and gilts following BFP was summarised as seven hour time interval. Pre-lying behaviour (see below for a definition), was calculated for each consecutive sample hour of the post-BFP observations.

The post-farrowing behavioural time budget data was not divided into smaller time samples, as for earlier Chapters, in order to simplify the analysis in the light of what is known about crushing. Crushing deaths occur throughout lactation whereas the majority of savaging occurs on the day of parturition (see Chapter 5). The behaviour of sows relating to risk of crushing appears to be consistent over a lactation (Wechsler and Hegglin, 1997), therefore splitting the post-farrowing period into smaller units for analysis would probably provide little additional information.

Piglet behaviour and location was measured on a whole litter basis using scan samples every 5 minutes following the onset of parturition and during the sow observation times. This data was summarised as for the sow and gilt behaviour.

For definitions of the behavioural categories recorded, see Chapter 2, Tables 2.6, 2.7 and 2.8.

Statistical Analysis

State-Lag Sequential Analyses and Time-Lag Sequential Analyses (Observer, Noldus Information Technology B.V., The Netherlands) were used to help identify posture changes associated with a crush or a 'near-miss' event. The Lag Sequential Analysis program could only deal with strings of two events, so it was essential to differentiate lying postures that followed other lying postures from lying postures that followed a stand, sit or kneel posture. This was done by constructing a Fortran 90 program (see Ellis *et al.*, 1994 for a description of this programming language), which re-named lie events that followed other lie events. Time-Lag Sequential Analyses counted all the 'near-miss' and crush events 10 seconds before a lying down manoeuvre was completed (e.g. during lying down) and 30 seconds after the lying position was achieved. This accounted for instances where a near-miss or crush was accidentally registered prior to the final lying posture being recorded. A State-Lag Sequential Analysis was then used to allocate any unaccounted crush and 'near-miss' events to a preceding posture (in the case of stand, sit or kneel) or posture change (in the case of lying down or changing lying postures).

Time-Lag Sequential Analysis was used to measure the amount of piglet-directed behaviour prior to lying down. Counts of looking at piglets, nose to nose contacts, nose to body contacts and rooting piglets were made during 60 seconds, 30 seconds and 10 seconds prior to each lie posture that followed a lying-down event. For each hour of the post-farrowing observation period, a value of mean amount of total piglet-directed pre-lying behaviour was calculated for each time lag (e.g. see equation 1 for a definition of Pre-lie$_{60}$, similar equations were calculated for Pre-lie$_{30}$ and Pre-lie$_{10}$).

In addition to these measures a weighted index of pre-lying behaviour, Pre-lie$_T$, was created that gave higher values to sows that did most of their pre-lying behaviour immediately before lying (see equation 2). It was hypothesised that piglet-directed behaviour immediately prior to lying was more effective at minimising the risk of piglet crushing than piglet-directed pre-lying behaviour performed at greater time latencies. If pre-lying behaviour influences the risk of crushing, a comparison of Pre-lie$_{60}$ with Pre-lie$_T$ would help answer this hypothesis.

Samples hours where no lying events occurred were classed as missing samples so that the variation in pre-lying behaviour could be assessed. It was hypothesised that sows with high scores for Pre-lie$_{60}$, Pre-lie$_{30}$, Pre-lie$_{10}$ and Pre-lie$_T$ would be more successful at avoiding crushing their piglets. This hypothesis assumes that sows do not intentionally crush piglets.

Amount of piglet-directed behaviour 60 seconds prior to lying, **Pre-lie$_{60}$**	=	$\frac{(\sum \text{nose, touch, root, look-at})/\text{hour}}{\text{No. Lying events/hour}}$

Equation 1

Summed pre-lying behaviour at 60, 30, and 10 seconds prior to lying, **Pre-lie$_T$**	=	Pre-lie$_{60}$ + Pre-lie$_{30}$ + Pre-lie$_{10}$

Equation 2

All behavioural measures, including the pre-lying behaviour measures, were entered into a Canonical Variates Analysis (CVA) that attempted to discriminate between the following groups:

Sow/gilt Category	Definition
CC	Sows that crushed two or more piglets to death during a single farrowing and lactation (n = 9)
C	Sows that crushed one piglet to death during a single farrowing and lactation (n = 27)
LO	Sows that did not crush piglets to death but were seen either laying on a piglet or on more than one occasion a piglet was witnessed having to move rapidly in order to avoid being crushed ('near-miss') (n = 51)
N	Sows that did not crush piglets to death and were not seen laying on a piglet during the sample periods. Sows in this group may have a maximum of one 'near-miss' attributed to them (n = 72).

For definitions of 'near-miss' and 'crush' events, see Chapter 2, Table 2.7.

Drawing the boundaries for the grouping of sows can be very subjective. In this case it was decided to distinguish between sows that crushed once from sows that crushed more than once because of the influence piglet viability has on the crushing statistics (English and Morrison, 1984). For instance, between groups 2 and 3 (C and LO) the only difference between a piglet being crushed to death or not could be whether the piglet that has been laid on is strong enough to free itself. The more frequently crushing deaths happen within a litter, the more sure we are that the crushing has something to do with the sows behaviour or the litter as a whole (e.g. a litter of low viability piglets). Group 4 (N), which includes sows with no crushing mortalities and were not seen laying on a piglet, also includes sows that may have almost crushed a piglet if it were not for the piglet moving away at the last minute. This recognises the fact that on some occasions, no matter how careful a sow is when she changes posture, a piglet may enter the area where the sow intends to lie at the last instance

and a near-miss may be recorded. The more frequently near-misses are recorded the more sure we are that the near missing is due to the sows behaviour.

Heavily loaded behaviours on all canonical variates, but paying more attention to the canonical variate that described the majority of the variation, were then tested for significant group differences using Residual Maximum Likelihood tests (REML). Behaviours with low loadings across all canonical variates were not analysed. The REML fixed model controlled for breed, parity, treatment, season, litter size and other non-experimental (uncontrolled) factors (see Table 4.1 in Chapter 4 for a complete list of these factors). A random model was also fitted that accounted for the repeated measures (sow/parity).

CVA's and subsequent REML tests were performed on the four pre-farrowing blocks and on the entire collated behavioural data following the onset of parturition.

The occurrence of litters with crushed piglets in relation to when during the day the sow farrowed was explored using a Chi-squared test. A two by two contingency Table was set up for number of litters with or without crushed piglets and born during the day (07:01 - 19:00 hours) or night (19:01 - 07:00 hours).

Chi-squared tests were also used to explore the frequencies of 'near-miss' and 'crush' events that followed different posture changes.

The relationship between degree of sibling competition and the incidence of crushing was explored by looking at crushing group differences (see above) for measures thought to be associated with sibling competition. These were:

1. Litter size, especially numbers born alive
2. Proportion of the litter active at the udder (teat massage and jostling for position)
3. Proportion of the litter inactive at the udder
4. Proportion of the litter active away from the sow or creep (fighting or exploring)
5. Proportion of the litter inactive away from the sow or creep (not including dead piglets)

Results

The Crushing Data

From 159 farrowings, 1643 piglets were born alive and 46 (2.8%) were later crushed. In 36 farrowings (22.6%), the sow crushed at least one piglet and in 16 of the farrowings with crushings (44.4%), a crushing occurred during a period of behaviour sampling. In addition to these crushings there were 76 observed instances when a sow lay on top of a piglet (defined as 'crush' in the ethogram, Chapter 2, Table 2.7) and 180 observed instances when a piglet had to move out of the way of a sow at the last instance to avoid being laid on.

Since less than half of the crushing deaths occurred during behavioural observation, the power of this study to identify behaviour resulting in crushing is limited. For behavioural characteristics of sows measured on the day of parturition to be predictive of crushing during the entire lactational period, behavioural predictors of crushing on the first day need to be consistent within individuals over time.

The Influence of Time of Day on the Incidence of Crushing

Parturitions were not confined to a particular time of day. There were 96 parturitions that began during the largely daylight hours between 07:00 and 19:00, and 63 parturitions that began between the mainly dark hours of 19:00 and 07:00. As well as coinciding roughly with daytime and night-time, 07:00 to 19:00 encompassed the times when farm staff were usually present and checking on the progress of parturition. Sows were fed at approximately 08:00 hours.

Crushing was more common in litters born during the day (27 litters, 28.1% of day-time farrowings, 07:01 - 19:00) compared to litters born during the night (9 litters, 14.3% of night-time farrowings, 19:01 - 07:00) ($\chi^2 = 4.16$, d.f. = 1, $p<0.05$; see Table 7.1). Table 7.1 illustrates how the parturitions of sows that crush piglets are more likely to begin during daylight hours than during night-time hours. The frequencies in

some of the cells in this Table were too small to do a 4 by 4 Chi-squared, so a 2 by 2 Chi-squared based on day versus night and crush versus no crush was calculated.

Table 7.1: The distribution of parturition times for sows that crush piglets (one or more than one) and sows that do not crush but were seen either laying on a piglet or almost laying on a piglet. The percentage of all farrowings during a particular time period that fall into one of the four crushing group categories are shown in brackets.

Crush group	**Time of Day Parturition Starts**			
	07:01 – 13:00	**13:01 – 19:00**	**19:01 – 01:00**	**01:01 – 07:00**
Crushes 2 or more piglets (CC)	3 (9.1%)	5 (7.9%)	1 (2.9%)	0 (0%)
Crushes 1 piglet (C)	6 (18.1%)	13 (20.6%)	4 (11.4%)	4 (14.3%)
Lays on a piglet but does not crush (LO)	12 (36.4%)	18 (28.6%)	13 (37.1%)	8 (28.6%)
Neither lays on a piglet nor crushes (N)	12 (36.4%)	27 (42.9%)	17 (48.6%)	16 (57.1%)

The Influence of Litter Size on the Incidence of Crushing

Degree of sibling competition, for space at the udder and access to a teat, will increase with litter size (de Passille and Rushen, 1989). In Chapter 5, a tendency ($p = 0.065$) was found for litter size to co-vary with the mean number of crushing mortalities per litter. Similarly, a weak association between the mean litter size of CC sows and gilts being larger than the mean litter size of N sows and gilts ($t_{79} = 2.04$, $p<0.05$). However, there was no difference between the four crushing groups in the mean number born alive (CC versus N, $p<0.20$) (see Table 7.2).

Table 7.2: The mean litter size of sows in the four crushing groups (described above and summarised in the Table). Values are back-transformed REML estimates controlled for repeated measures, breed, parity, season, treatment, age of sow and the time of day parturition started. Means with different superscripts differ significantly at $p<0.05$.

Crush Group	Mean litter size (+/- standard error)	Born alive (+/- standard error)
2 or more crushing mortalities (CC)	12.7 +/- 0.9[a]	11.8 +/- 0.9[a]
1 crushing mortality (C)	11.5 +/- 0.6[ab]	10.2 +/- 0.6[a]
No crushing mortalities but sow observed lying on a piglet (LO)	11.5 +/- 0.4[ab]	10.8 +/- 0.4[a]
No crushing mortalities and sow not seen lying on a piglet (N)	11.1 +/- 0.4[b]	10.6 +/- 0.4[a]

Posture Changes Associated with Crush and Near-miss Events

With this data set, it was possible to see what posture preceded a crushing or a near-miss event, and whether the sow responded to the crushing by moving off the piglet within 60 seconds (crush response) or not (crush no response). Table 7.3 presents this data, collated over the two parities and four breeds. Other posture changes not covered in this Table will be discussed later.

Table 7.3: Collated data from 159 sow farrowings. The number of crushes and 'near-misses' immediately following a particular posture change or posture (percentage of posture changes in brackets). Postural changes involving moving from a stand, sit or kneel position to a lying position (either lateral or ventral) are separated from postural changes that involve moving from one lying posture to another lying posture. Near-miss and crush events that follow a stand, sit or kneel posture are also presented.

Preceding Posture or Posture Change	**Frequency of occurrence**	**Following Event**			
		Near-miss	**Crush**	**Crush no response**	**Crush response**
Lying down to a lateral lying posture	1524	42 (2.8%)	15 (1.0%)	10	5
Lying down to a ventral lying posture	1902	49 (2.6%)	27 (1.4%)	9	18
Changing lying postures:					
Ventral - lateral	1268	7 (0.6%)	6 (0.5%)	4	2
Other	1204	5 (0.4%)	2 (0.2%)	1	1
Stand	1283	7 (0.5%)	5 (0.4%)	1	4
Sit	2158	21 (1.0%)	14 (0.6%)	6	8
Kneel	933	49 (5.3%)	7 (0.8%)	7	0

This data provides an indication of what postural changes are associated with an increased risk of crushing but the frequencies do not take into account repeated measures, parity, breed, age of sow, season, time of day, litter size and treatment differences between litters. All these factors may influence the likelihood of a particular postural change resulting in a crush or near-miss event. These factors will be accounted for later when the behaviour associated with the different crushing groups will be presented.

Crushing events happened too infrequently to be used in an integrated parametric analysis to identify breed, parity and straw effects. However, near-miss events could be analysed in this way. There were no parity or straw effects on the frequency with

which a sow would almost crush a piglet but breed differences were apparent. Meishan-Landrace (50% Meishan) sows had more near-miss events than either Landrace-Duroc (t_{86} = 3.1, $p<0.01$) or Duroc sows (t_{124} = 3.2, $p<0.01$) (see Figure 7.1). The frequency with which a sow would almost crush a piglet on the day of parturition was not consistent over parities. These near-miss events can be associated with the type of posture change or posture preceding them on a breed by breed basis (see Table 7.4).

Figure 7.1: Breed differences, after controlling for litter size, parity and season, in the frequency of near-miss (near-crush) events per hour on the day of parturition. Error bars show the 95% confidence intervals. ** = $p<0.01$

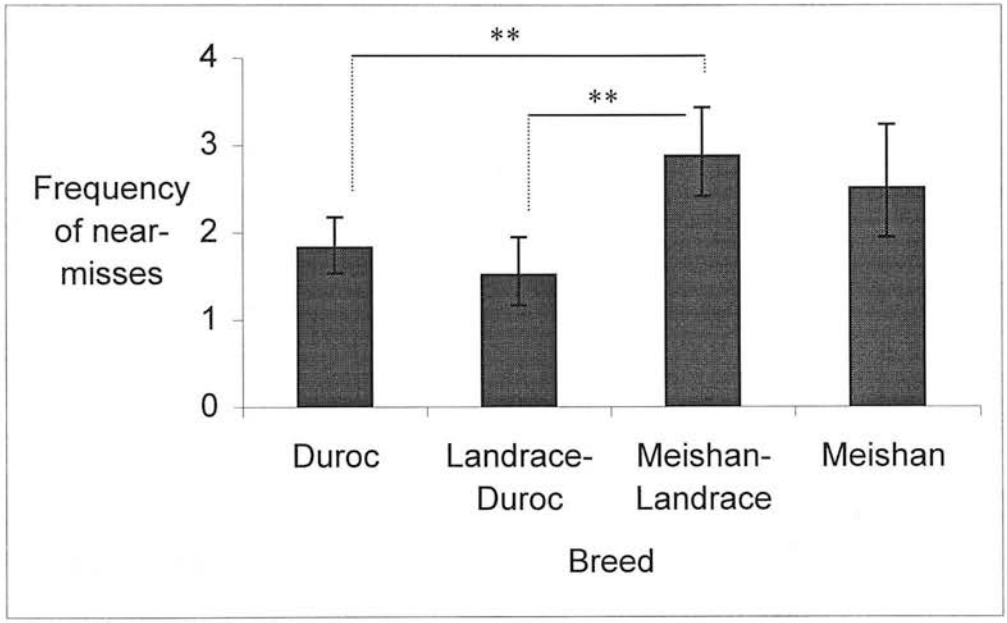


Table 7.4: Posture changes and postures preceding near-miss piglet crushing events. The Table divides the near-miss data from Table 7.3 (3rd column) into the four different breeds.

Preceding Posture or Posture Change	**Frequency (percentage) with which posture or posture change is followed by a near-miss (near-crush) event**			
	Duroc	**Landrace-Duroc**	**Meishan-Landrace**	**Meishan**
Lying down to a lateral lying posture	12 (2.6%)	1 (0.7%)	28 (3.5%)	1 (1.4%)
Lying down to a ventral lying posture	14 (2.6%)	4 (2.9%)	26 (2.6%)	5 (2.5%)
Changing lying posture:				
Ventral to lateral	2 (0.5%)	0 (0%)	4 (0.6%)	1 (0.5%)
Other	0 (0%)	1 (2.5%)	4 (0.8%)	0 (0%)
Stand	0 (0%)	1 (0.7%)	6 (1.0%)	0 (0%)
Sit	4 (0.7%)	0 (0%)	15 (1.3%)	2 (1.0%)
Kneel	19 (5.5%)	2 (2.4%)	25 (6.7%)	3 (5.4%)

The data presented in Table 7.3 seemed to suggest that a sow was more likely to respond to crushing events after lying down to a ventral position than after lying down to a lateral position. This was tested by performing a Chi-squared test on the data after first adjusting the frequencies in each cell to be independent. Four sows contributed twice to the same cell in the contingency Table, and these crush events occurred close together in time (less than 1 hour), making them unlikely to be independent (Martin and Bateson, 1993). After removing these non-independent repeated measures on the same sow, the contingency Table was as follows:

	Crush no response	Crush response
Lying down to a lateral lying posture	6	4
Lying down to a ventral lying posture	8	13

The chi-squared value from this contingency Table was smaller (1.3) than the critical value (3.14) and so the ratio of 'crush responses' to 'crush no responses' was not higher after lying down ventrally than after lying down laterally.

There appeared to be more crush events, and in particular crush no response events, following rolling (ventral-lateral) compared to any other type of changing posture whilst lying (see Table 7.3). However, crush events were associated with changing lying postures too infrequently to apply a Chi-squared test as above.

Many crush and near-miss events were not associated with either lying down or changing posture whilst lying (see Table 7.3). For these events the last posture was either stand (7 near-misses, 5 crushes), sit (21 near-misses, 14 crushes) or kneel (49 near-misses, 7 crushes). Kneel was most likely to be followed by a crush or a near-miss event. The kneel posture is almost always associated with lying down: 49% of all posture changes involving kneel were of the stand to kneel type, whilst a further 42% were of the kneel to lie type. Therefore it is likely that the near-miss and crush events that followed a kneel posture were associated with lying down from a standing position. The majority of all posture changes that ended with the sit posture are of the lie to sit type (99.4%), whilst 0.5% (10 occasions for all sows) are of the stand to sit type. Therefore it is likely that the near-miss and crush events that followed a sit posture will have been associated with a lie to sit posture change. Instances where crush or near-miss was preceded by a stand posture indicate the sow stepping or almost stepping on a piglet. Although it is also possible, in the crush response cases, that stand was the sows response to laying on a piglet.

Piglet-directed Pre-lying Behaviour

The amount of piglet-directed behaviour prior to lying during the period of observation had very little influence on whether a sow crushed prior to piglet weaning (see Figure 7.2). This was true of all observation hours following the onset of parturition except for the third hour when sows that crushed two or more piglets (CC) did marginally less pre-lying behaviour (Pre-lie$_T$) than sows that did not crush piglets (N) ($t_{79} = 2.3$, $p<0.05$) (see Figure 7.2). Similar results were found for piglet-directed behaviour 60 seconds prior to lying (Pre-lie$_{60}$) and 30 seconds prior to lying (Pre-lie$_{30}$). Sows with piglet-directed pre-lying behaviour 10 seconds prior to entering the lying posture were very rare, and consequently were not suitable for parametric analysis.

Pre-lying behaviour was not affected by litter size, parity, age of the sow or the presence of

straw. There were significant breed differences with Duroc sows doing significantly less piglet-directed behaviour per lie than Meishan-Landrace sows ($t_{124} = 4.1$, $p<0.001$) (see Figure 7.3). Pre-lying behaviour was not found to be consistent within sows over parities one and two.

Figure 7.2: Mean amount of piglet-directed pre-lying behaviour (+/- 95% confidence intervals) during the six hours following the onset of parturition (sample hours 1-6) and during the six 10-minute samples at 9, 12, 15, 18, 21 and 24 hours following the birth of the first piglet. The pre-lying behaviour measure shown is Pre-lie$_T$ (see equation 2, methods), back-transformed from the REML estimates that controlled for repeated measures, breed, treatment, parity, season, age of sow, litter size and time of day. Data for two groups of sows are presented - sows that crushed 2 or more piglets (CC, n = 9) and sows that did not crush but may have had one 'near-miss' (N, n = 72). * = $p<0.05$

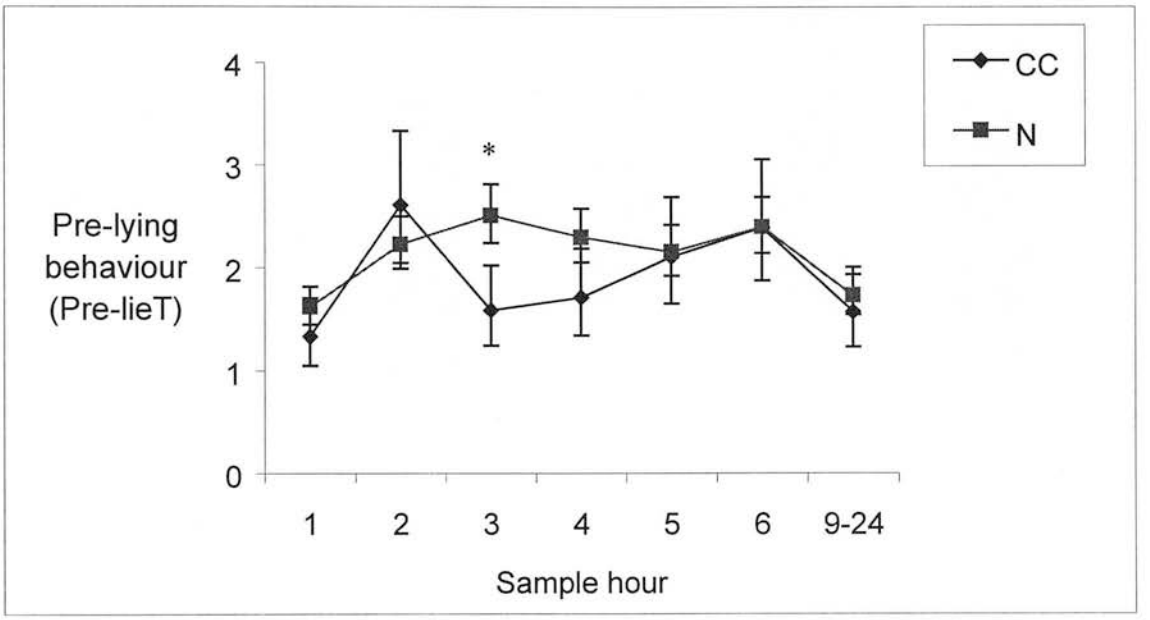
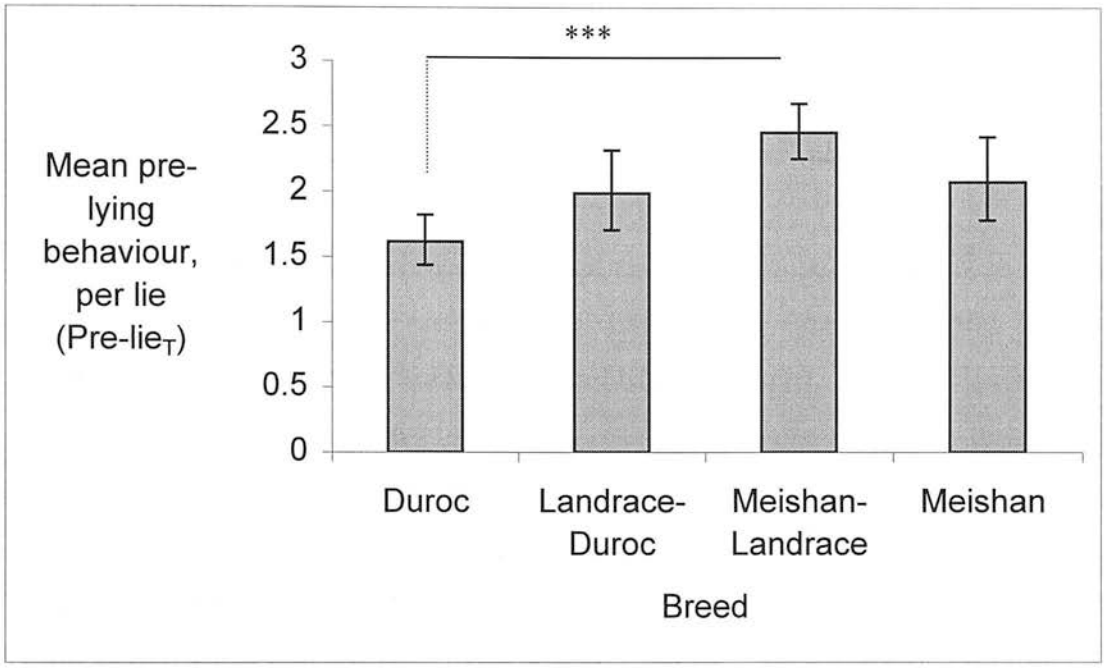


Figure 7.3: Breed differences, controlled for parity, age, season and litter size, in the mean amount of piglet-directed pre-lying behaviour per hour on the day of parturition (with 95% confidence intervals). Out of 159 sow farrowings, all but 8 sows lay down at least once during the observation periods.

*** = $p<0.001$.



Other Behaviours Associated with Crushing

Pre-farrowing Behaviour

Four Canonical Variates Analyses (CVA) were performed on the pre-farrowing behaviour data - one for each of the collated time blocks as described in the methods. The CVA generated three canonical variates for each time block. The grouping factor used was based on the number of piglets a sow crushed and whether she was seen lying on a piglet or not. As detailed in the methods.

Crushing groups CC and N were not always found at opposite extremes in the canonical variate means produced for each pre-farrowing time block. In these cases a combination of two canonical variates were necessary to distinguish CC sows from N sows. When a canonical variate did separate CC from N, leaving sows in groups C

and LO with intermediate values, the amount of between group variance explained was relatively small (approximately 40%). This indicates that much of the variation between sows (and gilts) in their pre-farrowing behaviour can not be explained by what crushing group the sow or gilt belonged.

Differences were observed between the crushing groups in their expression of pre-farrowing behaviour. The majority of these differences were before (-24, -20 hours) and after (-4, -2, 0 hours) the main period of when most sows nest-build (see Chapter 3) and these differences centred around how active the sows were.

Figure 7.5 illustrates the differences between crushing groups CC and N in the time spent inactive during each pre-farrowing time block (groups C and LO had intermediate values and were omitted to simplify the graph). Table 7.5 presents the inactivity data for all four crushing groups over all four pre-farrowing time blocks. Figure 7.6 illustrates crushing group differences during -24 and -20 hours pre-farrowing in the frequency of sitting up. Figure 7.7 illustrates the crushing group differences in time spent interacting with the straw or floor of the farrowing crate during -4 to 0 hours pre-farrowing.

Table 7.5: Differences between the crushing groups (for definitions see methods) in the time spent inactive during the pre-farrowing period. Means are back-transformed REML estimates (95% confidence intervals in brackets) controlled for repeated measures, breed, parity, treatment, season, litter size, age of sow, time in crate prior to farrowing and time of day farrowing starts. Means with different superscripts differ significantly at $p<0.05$ within a time period and between crushing groups.

Crushing Group	Pre-farrowing Time Block			
	-24, -20	**-16, -14, -12**	**-10, -8, -6**	**-4, -2, 0**
CC	93.1%^{a} (84.8 - 98.3%)	66.6%^{a} (54.5 - 77.6%)	17.4%^{a} (9.5 - 27.0%)	27.5%^{a} (18.5 - 35.1%)
C	67.4%^{b} (57.7 - 76.4%)	38.4%^{b} (29.3 - 47.9%)	23.3%^{a} (16.1 - 31.3%)	38.8%^{ab} (30.7 - 47.1%)
LO	74.7%^{b} (65.6 - 82.9%)	54.9%^{ab} (45.3 - 64.3%)	27.4%^{a} (19.8 - 35.8%)	36.5%^{ab} (28.6 - 44.8%)
N	70.4%^{b} (62.5 - 77.8%)	49.3%^{ab} (43.3 - 55.4%)	25.6%^{a} (21.0 - 30.5%)	43.8%^{b} (36.5 - 51.2%)

Sows and gilts that crushed two or more piglets (CC) spent more time inactive during -24 and -20 hours ($t_{35} = 2.8$, $p<0.01$) and -16 to -12 hours ($t_{35} = 2.3$, $p<0.05$) than sows and gilts that crushed one piglet (C). In addition, sows and gilts that crushed two or more piglets (CC), spent more time inactive during -24 and -20 hours than sows and gilts that did not crush piglets (LO, $t_{58} = 2.8$, $p<0.01$; N, $t_{79} = 3.3$, $p<0.01$) (see Table 7.5 and Figure 7.4). Between -10 and -6 hours, there were no behavioural differences between any of the crushing groups. Between -4 to 0 hours, sows that crushed two or more piglets (CC) spent less time inactive than sows that neither crushed nor were seen to lay on a piglet (N) ($t_{79} = 2.4$, $p<0.05$; see Table 7.5 and Figure 7.5).

During -24 to -20 hours pre-farrowing, sows that crushed two or more piglets (CC), sat up (lie - sit) less frequently than other sows (C, $t_{35} = 1.8$, $p<0.1$; LO, $t_{58} = 2.7$, $p<0.02$; N, $t_{79} = 4.1$, $p<0.001$; see Figure 7.5).

Figure 7.4: The proportion of time spent inactive (+/- 95% confidence intervals). Means are back-transformed REML estimates (95% confidence intervals in brackets) controlled for repeated measures, breed, parity, treatment, season, litter size, age of sow, time in crate prior to farrowing and time of day farrowing starts. Only two crushing groups are shown, CC and N; the other two groups (C and LO) had intermediate values and are omitted to simplify the graph. Crush group CC contains 9 sows that crushed more than one piglet, crush N contains 72 sows that neither crushed nor were seen to lie on a piglet.

** = $p<0.01$, * = $p<0.05$

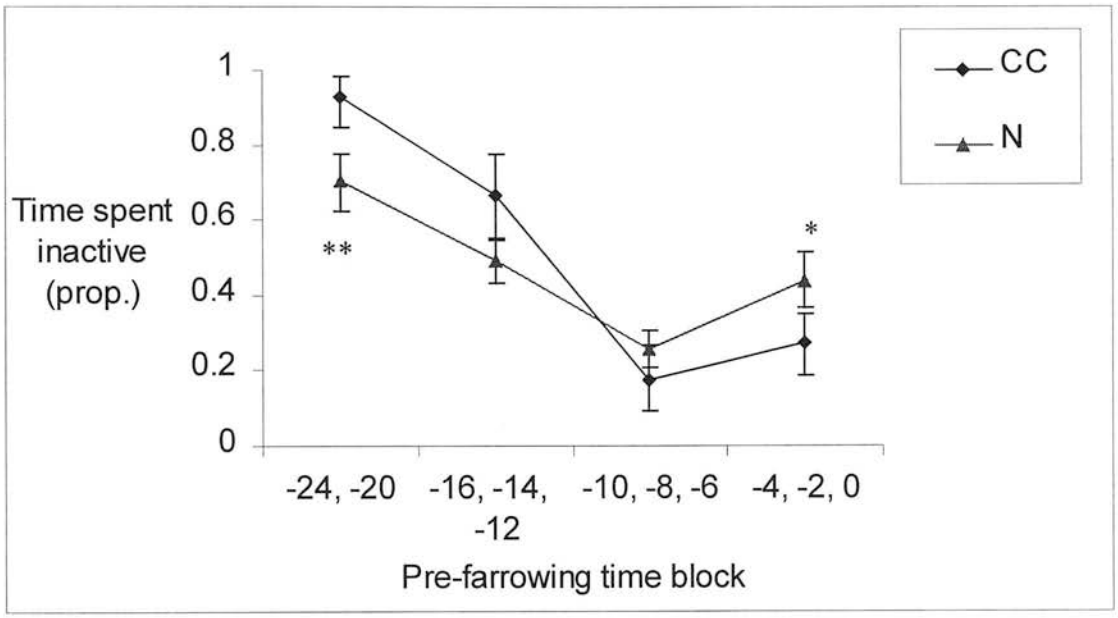
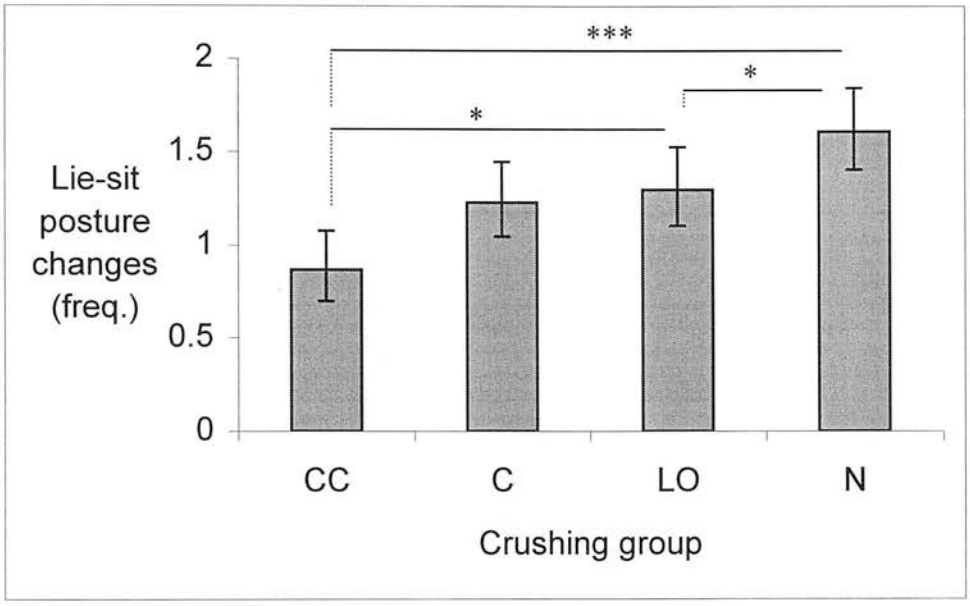


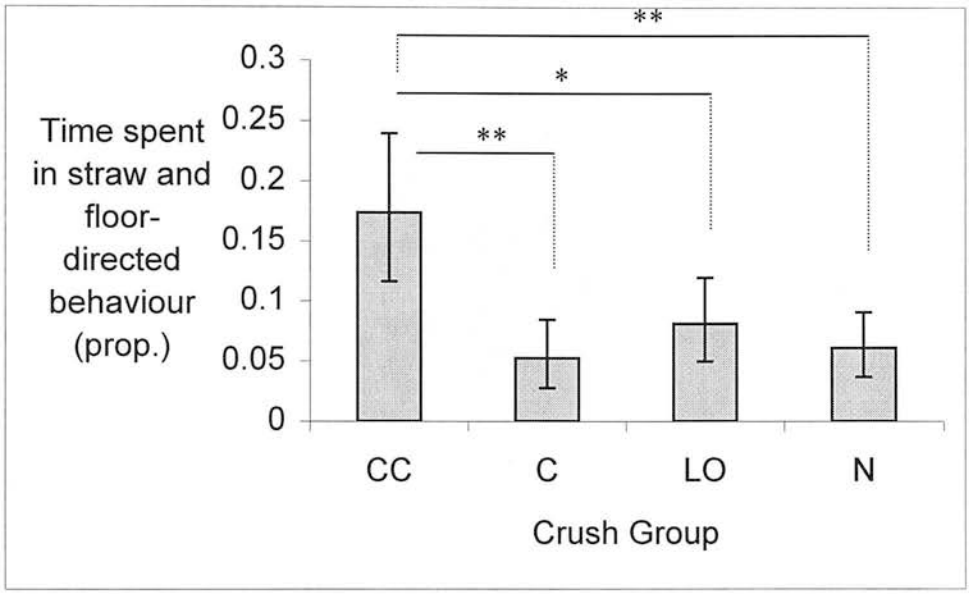
Figure 7.5: Mean frequency of lie - sit posture changes (+/- 95% confidence intervals), during the -24 and -20 hour pre-farrowing samples (multiplied up to be equivalent to 30 minutes of sample time). Values are corrected for time of day, breed, parity, season, age, treatment and farrowing house; and adjusted for repeated measures. Means are presented for the four crushing groups described in the text.

* = $p<0.05$, *** = $p<0.001$



The expression of straw and floor-directed behaviour also varied between crushing groups but only between -4 and 0 hours pre-farrowing. During this time period, sows that crushed two or more piglets spent more time engaged in straw or floor-directed behaviour than the other groups of sows (CC versus C, $t_{35} = 2.8$, $p<0.01$; CC versus LO, $t_{58} = 2.6$, $p<0.02$; CC versus N, $t_{79} = 3.3$, $p<0.01$; see Figure 7.6).

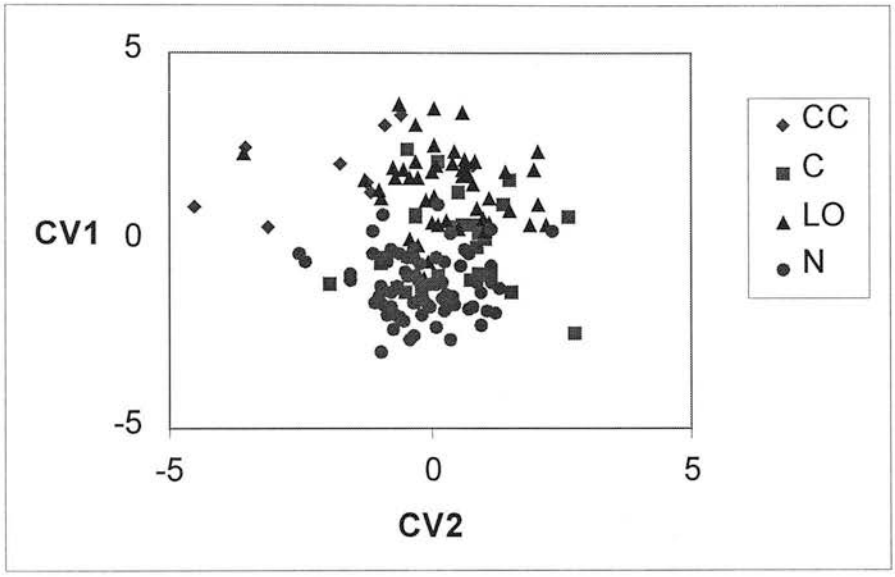
Figure 7.6: Mean time spent in straw and floor-directed behaviour (+/- 95% confidence intervals), between -4 and 0 hours pre-farrowing. The groups of sows shown are sows that crushed two or more piglets (CC), sows that crushed one piglet (C), sows that did not crush but laid on piglets (LO) and sows that did not crush and did not lay on piglets (N). Values are back-transformed REML estimates, controlled for repeated measures, breed, parity, treatment, season, age of sow, time in crate prior to farrowing, farrowing house and time of day farrowing starts. * = $p<0.05$, ** = $p<0.01$



Behaviour of the Sow or Gilt Following the Onset of Parturition

Thirty-two behavioural measures were entered into the Canonical Variates Analysis of behaviour following the birth of the first piglet, producing three canonical variates. The first two canonical variates explained 88.7% of the between group variation. The group means for the first canonical variate (75.4% variation) had crush groups CC and N at opposite extremes, whereas the group means for the second canonical variate (13.3%) had crush groups CC and C at opposite extremes. The third canonical variate (11.3% variation) attempted to discriminate between crush groups C and LO, although this was unsuccessful at the level of individual behaviours. Figure 7.8 shows how well the first two canonical variates separated the crush groups.

Figure 7.7: The distribution of sow farrowings, split into the 4 crush groups (described above), along the axes of the first two canonical variates (CV). Together, these first two canonical variates explained 89% of the between group variation in behaviour following the birth of the first piglet. CC - sows that crushed to death more than one piglet; C - sows that crushed to death one piglet; LO - sows with no crushing mortalities but were seen laying on a piglet or a piglet was almost crushed more than once; N - sows that had no crushing mortalities and were not seen laying on a piglet, piglet may have almost been laid on once.



Out of 32 behavioural measures entered into the CVA, 22 were then analysed for group differences on the basis of their CV1 and CV2 loadings using REML analyses of variance. Given the number of tests performed we might expect at least one difference to occur through chance alone. Therefore a probability level of $p<0.01$ would provide a better indicator of significant group differences.

Risk of crushing, as measured as differences between the crush groups, was influenced strongly by the frequency of posture changing. These differences are summarised in Table 7.6.

Table 7.6: Posture changes that were found to be significantly different ($p<0.05$) between the crushing groups. Mean numbers of posture changes are for 7 hours of observation, taken over 24 hours following the onset of parturition. The means are back-transformed from the REML estimates (95% confidence intervals in brackets), controlled for repeated measures, breed, season, parity, litter size, time of day, farrowing house and age of sow. Means with different superscripts are significantly different at $p<0.05$.

Posture Change	**Crushing Group Means (freq.)** (per 7 hours of sample time)			
	CC	**C**	**LO**	**N**
Lying down to a lateral lying posture (flop)	3.09^{a} (2.21 - 4.31)	1.78^{ab} (1.37 - 2.32)	2.63^{a} (2.04 - 3.45)	1.55^{b} (1.24 - 1.97)
Laying down to a ventral lying posture	9.33^{a} (6.36 - 13.53)	6.61^{a} (4.92 - 8.88)	6.66^{a} (4.96 - 8.95)	3.91^{b} (3.02 - 5.08)
Stand - kneel	4.96^{a} (3.32 - 7.39)	3.39^{a} (2.48 - 4.62)	3.84^{a} (2.81 - 5.24)	1.75^{b} (1.33 - 2.30)
Kneel - lie	5.70^{a} (3.88 - 8.37)	3.66^{a} (2.71 - 4.95)	4.40^{a} (3.26 - 5.95)	1.89^{b} (1.45 - 2.46)
Lie - sit	7.96^{a} (5.94 - 10.67)	4.84^{ab} (4.09 - 5.74)	5.80^{a} (5.13 - 6.55)	3.16^{b} (2.85 - 3.51)
Sit - stand	4.02^{a} (2.77 - 5.83)	2.71^{a} (2.03 - 3.62)	3.59^{a} (2.68 - 4.79)	1.52^{b} (1.18 - 1.97)
Ventral lie - lateral lie (roll)	7.18^{a} (5.29 - 9.74)	6.21^{ab} (4.89 - 7.89)	6.46^{a} (5.09 - 8.21)	4.67^{b} (3.78 - 5.78)

Not all posture changes showed significant differences between the groups. Frequencies of kneel to stand, lie to stand and sit to lie were all not significantly different between the groups.

Crushing group differences were present for standing up posture changes (lie-sit, sit-stand) but not for lying down from a sitting position. On the basis of this result, it was hypothesised that sows that crush piglets were more likely to make lie-sit-stand posture changes than lie-sit-lie posture changes. To test this hypothesis the proportion

of all lie-sit sequences that became lie-sit-stand sequences was calculated for each sow. Figure 7.8 shows the group differences for this behaviour measure.

Variation in the proportion of lie-sit sequences that become lie-sit-stand sequences was great, as might be expected if proportions are to be calculated from such low numbers as displayed in Table 7.6. There was no difference between crushing and non-crushing sows and gilts in the proportion of lie-sit sequences that become lie-sit-stand sequences. However, sows and gilts that were seen to either lay on a piglet or had two or more near-miss events on more than one occasion, were more likely to stand from a sitting posture than sows that were not seen laying on a piglet and had none or one near-miss events ($t_{121} = 3.45$, $p<0.001$) (see Figure 7.8).

Figure 7.8: The proportion of lie-sit sequences that become lie-sit-stand sequences (the alternative is lie-sit-lie). The back-transformed means from those estimated by REML, controlled for repeated measures, breed, treatment, parity, time of day, season, litter size, age of sow and farrowing house. Error bars show the 95% confidence intervals. *** = $p<0.001$

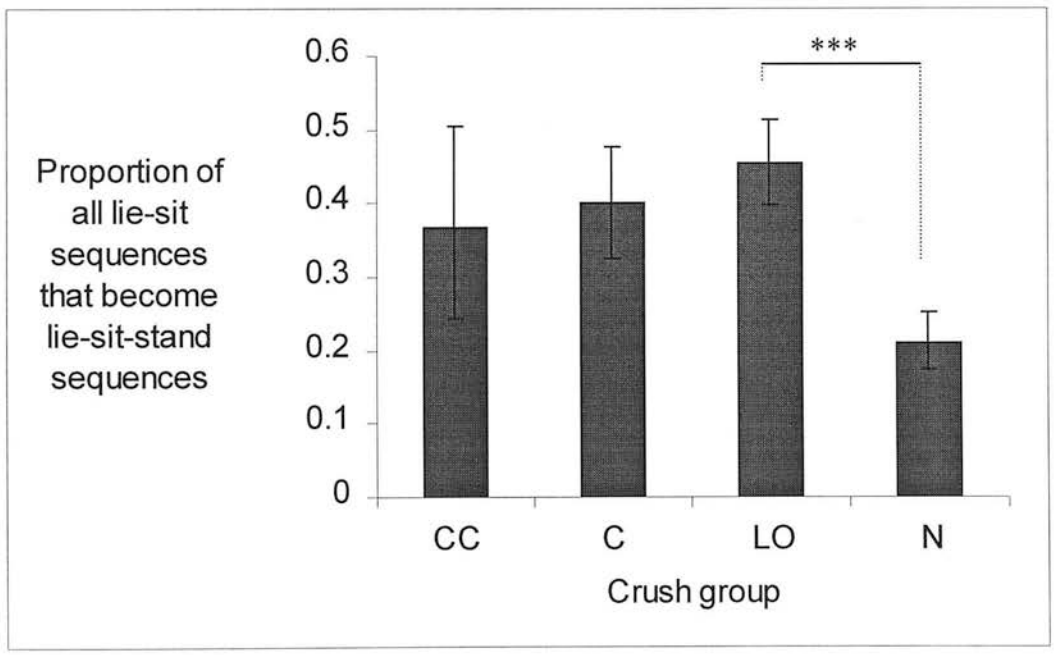
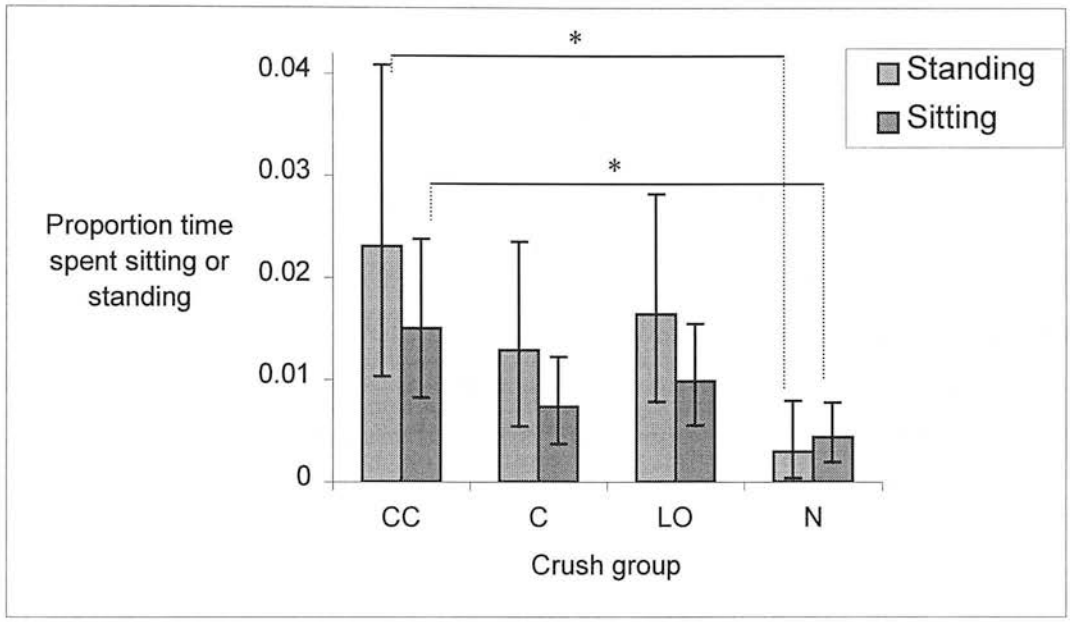


Figure 7.9: Differences between the 4 crushing groups in the proportion of the sample time (7 hours) spent in sitting and standing. Values are the back-transformed means of REML estimates, controlled for repeated measures, breed, treatment, parity, season, time of day and other non-experimental factors that influenced these behaviours. Error bars show the 95% confidence intervals. * = $p<0.05$



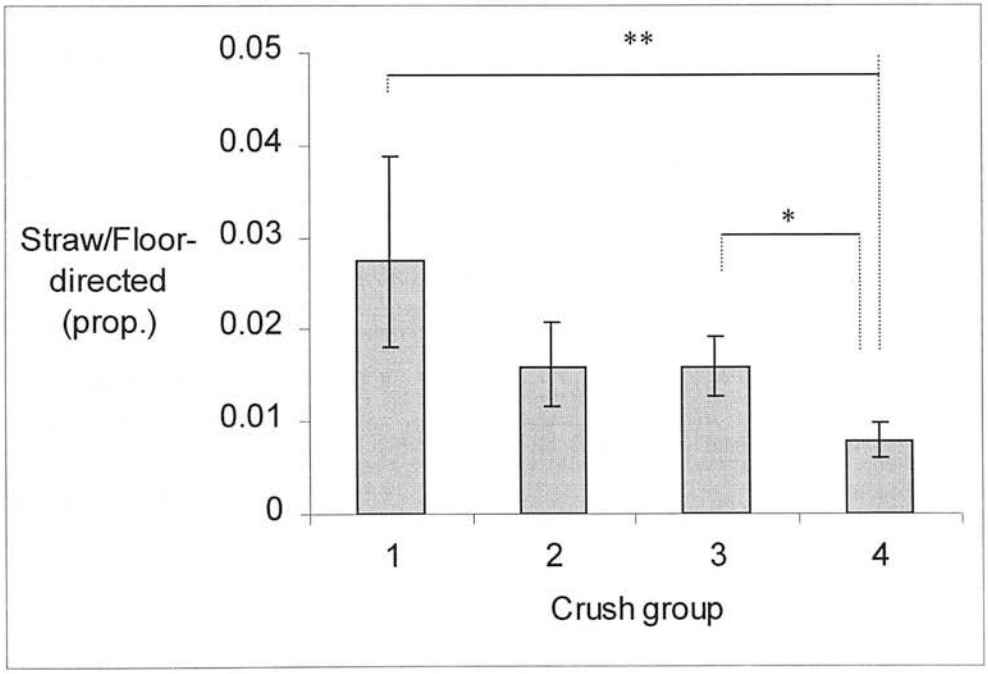
Sows and gilts that crushed two or more piglets (CC) spent more time in kneel, sit and stand postures than sows and gilts that neither crushed nor were seen laying on a piglet (N) (kneel - $t_{79} = 3.2$, $p<0.01$; sit - $t_{79} = 2.6$, $p<0.02$; stand - $t_{79} = 2.1$, $p<0.05$) (see Figure 7.9). Sows and gilts that were seen to lay on a piglet or almost crush a piglet more than once (LO) also spent more time in these postures than N sows and gilts (kneel - $t_{131} = 3.3$, $p<0.01$; sit - $t_{131} = 2.5$, $p<0.02$; stand - $t_{131} = 2.4$, $p<0.02$) (see Figure 7.9). There were no differences between the groups in the time spent lying either ventrally or laterally. Variability in these behaviour measures was great reflecting the dramatic changes in the activity of sows over the course of parturition (see Chapter 4).

Piglet-directed behaviours such as frequencies of rooting piglets, naso-naso contacts, nose to body contacts, not responding to piglets approaching the sows head or time spent looking at piglets did not differ between the crushing groups.

Once parturition had begun, straw and floor-directed behaviour occupied only a small proportion of the sow or gilts time (approximately 2% - see Figure 7.10). Sows and gilts that crushed two or more piglets (CC) spent more time in straw and floor-directed behaviour than sows and gilts that neither crushed nor were seen to lay on piglets (N) ($t_{79} = 2.76$, $p<0.01$) (see Figure 7.10). Sows and gilts that did not kill a piglet through crushing but were seen to lay on a piglet or almost crush a piglet on more than one occasion (LO) spent more time in straw/floor-directed behaviour than N sows ($t_{131} = 2.21$, $p<0.05$) (see Figure 7.10).

Figure 7.10: Differences between the four crushing groups in the proportion of time spent engaged in straw or floor-directed behaviour (+/- 95% confidence interval) during the 24 hours following the onset of parturition. Values are back-transformed REML estimates controlled for repeated measures, breed, treatment, parity, time of day, season, litter size, age of sow and farrowing house.

** = $p<0.01$, * = $p<0.05$



Behaviour and Location of the Litters of Crushing and Non-Crushing Sows and Gilts

There were no differences between the litters of sows and gilts from the different crushing groups in the time they spent in the creep, at the sows vulva, active away from the sow or creep. The measures of piglet behaviour and location that did vary between the crushing groups is summarised in Table 7.7.

Table 7.7: Differences between the four crushing groups in the behaviour and location of their litters. Values are back-transformed REML estimates (95% confidence intervals in brackets) controlled for repeated measures on the sow, breed and parity of the sow, season, litter size, length of parturition, farrowing house and whether a radio was playing in the house. Within each behaviour, means with different superscripts differ significantly at $p<0.05$ (t-distribution).

Piglet behaviour and location	**Crushing Group**			
	CC	**C**	**LO**	**N**
Active at the udder	$38.0\%^{a}$ (34.3 - 41.8%)	$42.5\%^{ab}$ (40.3 - 44.7%)	$43.0\%^{ab}$ (41.5 - 44.6%)	$48.3\%^{b}$ (47.0 - 49.7%)
Inactive at the udder	$9.8\%^{a}$ (8.0 - 11.7%)	$12.6\%^{ab}$ (11.4 - 13.8%)	$13.9\%^{b}$ (13.0 - 14.9%)	$14.3\%^{b}$ (13.5 - 15.1%)
Inactive away from the sow/gilt or creep	$14.5\%^{a}$ (11.8 - 17.5%)	$10.6\%^{ab}$ (9.3 - 12.1%)	$10.6\%^{ab}$ (9.6 - 11.6%)	$7.8\%^{b}$ (7.1 - 8.6%)
Underneath a standing or sitting sow or gilt	$0.4\%^{ab}$ (0.2 - 0.6%)	$0.4\%^{ab}$ (0.2 - 0.5%)	$0.6\%^{a}$ (0.5 - 0.8%)	$0.1\%^{b}$ (0.1 - 0.1%)

The litters of sows and gilts that crushed two or more piglets (CC) spent less time active at the udder ($t_{79} = 3.09$, $p<0.01$) and less time inactive at the udder ($t_{79} = 2.53$, $p<0.02$) than the litters of sows and gilts that neither crushed nor were observed lying on a piglet (N). In addition, the litters of CC sows and gilts spent less time inactive at

the udder than the litters of sows and gilts that did not crush but were observed lying on a piglet (LO) ($t_{58} = 2.34$, $p<0.05$).

The litters of CC sows and gilts spent more time inactive away from the udder than the litters of N sows and gilts ($t_{79} = 2.53$, $p<0.02$).

The litters of LO sows and gilts spent more time underneath a sitting or standing sow or gilt that the litters of N sows and gilts ($t_{121} = 4.88$, $p<0.001$).

Discussion

Sows that crushed once were indistinguishable in their behaviour from sows that did not crush but were seen either lying on a piglet or almost lying on a piglet on more than one occasion. This suggests that, in many instances, the crushing of piglets is accidental and indicates that the difference between sows recorded as crushers or non-crushers is sometimes not the behaviour of the sows but the viability of the piglets that were laid on. This is consistent with current thinking on the causes of crushing (Weary *et al.*, 1996b; English and Edwards, 1996).

The behaviour and location of the litters of crushing and non-crushing sows and gilts indicated that the viability of the litter as a whole, as measured by the time litters spent inactive away from the sow or creep, was lower for litters that had piglets crushed prior to weaning. This finding is consistent with the higher blood lactate levels at birth in piglets that subsequently died compared to piglets that were still alive at three weeks of age (English and Smith, 1975). Blood lactate level at birth is a measure of the degree of anoxia suffered during birth (Dawes *et al.*, 1963), whilst blood pH positively co-varies with piglet viability score (low score being equivalent to poor viability, which was associated with a low pH; Randall, 1971).

In support of Weary *et al.*'s (1996b) findings, the litters of sows that were observed lying on a piglet were more likely to be found in a position of high risk of crushing (underneath a sitting or standing sow) than the litters of sows that were never seen lying on a piglet. However, there was no difference between the litters of crushing and non-crushing sows and gilts in the time they spent underneath a sitting or standing sow, in contrast to Weary *et al.* (1996b). In addition, The litters of sows and gilts that crushed two or more piglets spent less time at the udder than the litters of non-crushing sows and gilts. This result highlights difficulties for the hypothesis that crushing results from piglets spending more time close to the sow in an attempt increase their intake of milk (Fraser, 1990; Weary *et al.*, 1996b). However, the behaviour of the sow should also be taken into account, for example, more time spent standing or sitting will reduce the opportunity of their litters to spend time near the udder.

Litters that contained crushed piglets were more likely to be born during the day (07:01 – 19:00 hours), when farm staff were available, than during the night (19:01 – 07:00 hours), when sows were undisturbed. This is inconsistent with the belief that having farm staff attend and assist the sow at parturition can reduce the overall piglet mortality (Nickerson, 1996; Hacker, 2000). In Chapter 4 data is presented showing that the frequency of posture changing was higher for sows whose parturitions occurred close to the morning food delivery. The higher incidence of crushed piglets amongst litters born during the day is likely to be due to the increased activity of sows during the day; either through natural diurnal rhythms modified by set feeding times or by human disturbance. Therefore, in order to minimise the risk of crushing, efforts should be made not to disturb the sow unnecessarily during parturition. One way of achieving this would be to make the food available continuously, allowing the sow or gilt to choose when to eat.

The litter size of sows and gilts that crushed two or more piglets was slightly higher than the litter size of sows and gilts that neither crushed nor were seen to lay on a piglet, supporting the tendency found in Chapter 5. This is also consistent with Wechsler and Hegglin's (1997) suggestion that a high litter size is a risk factor for crushing. However, this difference between crushing and non-crushing sows did not hold for numbers born alive, which is inconsistent with the hypothesis that risk of crushing is related to the number of piglets the sow must avoid when she lies down (Wechsler and Hegglin, 1997). Risk of crushing is likely to influenced by many factors such as the behaviour of the litter (Weary *et al.*, 1996b) and the behaviour of the sow (Marchant *et al.*, 1996; Weary *et al.*, 1996a; Wechsler and Hegglin, 1997).

The litters of multiple crushers spent less time active at the udder than the litters of non-crushing sows, whilst there were no differences in the time spent active away from the sow or creep. These findings provide no evidence of higher levels of sibling competition amongst litters with crushed piglets, contrary to previous work (English and Smith, 1975; Hartsock and Graves, 1976; Fraser, 1990). However, the litters of crushing and non-crushing sows also differed in their overall viability, as measured by time spent inactive away from the sow or creep, which will confound any effects differences in the degree of sibling competition may have.

A high frequency of posture changing was a major characteristic of sows that crushed piglets. However, not all types of posture change were associated with sows that crushed. One posture change previously found to be associated with piglet crushing in farrowing crates, sit to lie (Edwards *et al.*, 1986), did not differ in frequency between sows that crush two or more piglets and sows that did not crush. However, lie to sit was more frequent amongst multiple crushers than amongst non-crushing sows, suggesting that multiple crushers were more likely to stand up rather than lie back down once in a sitting posture. Several crush and near-miss events were preceded by lie to sit posture changes, supporting what others have found (Weary *et al.,* 1996a). Lying down from standing (stand to kneel to lie) was most likely, of all the postural changes, to be followed by a crush or near-miss event and was strongly associated with the behaviour of sows and gilts that crushed two or more piglets, along with standing up postural changes. Thus, standing up and lying back down again leads to a greater risk of piglet crushing than sitting up and lying back down again. This finding does not support the work of Edwards *et al.* (1986), who found that sitting up and lying back down again (lie-sit-lie) was the main posture change sequence responsible for the majority of crushed piglets in farrowing crates (Prof. S. A. Edwards, pers. comm.). The discrepancy between the current study and the Edwards *et al.* (1986) study could be due to subtle differences between the type of farrowing crates used, possibly leading to more sitting up in the earlier study. The reason why lying down from a kneeling position is associated with a greater risk of crushing than lying down from a sitting position could be that the location of piglets could be easier to see when sitting compared to kneeling.

When lying down, a sow can elect to either descend to a ventral lying posture or a lateral lying posture. In this study lying down to a ventral posture was more common than lying down to a lateral posture. This is likely to be an effect of the farrowing crate, which was designed to reduce the occurrence of lying down to a lateral lying posture (English *et al.*, 1977, p. 135; Green, 1981; Baxter, 1984, p. 455). Wechsler and Hegglin (1997) found that, for sows in pens, lying down to a lateral posture was a more dangerous movement, in terms of risk of crushing, than lying down to a ventral posture. The data from this study would suggest that this is not the case for sows in farrowing crates. If the sow has laid down to a ventral lying posture, in order to suckle

her piglets, a sow must roll onto her side (ventral to lateral lie). This rolling posture change has been equated with an increased risk of crushing when sows are kept in pens (Weary *et al.*, 1996a; Wechsler and Hegglin, 1997; Weary *et al.*, 1998). The data from this study demonstrates that, for sows in crates, this posture change is no more dangerous than any other postural change that occurs whilst the sow is in a lying position. One might conclude from these results that the farrowing crate has successfully reduced the impact of two types of posture change thought to have a high risk of crushing: a) lying down to a lateral posture, and b) moving from a ventral to a lateral lying posture.

In contrast to the behaviour of savaging gilts (see Chapter 6), there were few pre-farrowing behavioural differences between crushing and non-crushing sows. This supports the finding of Chapter 5 that crushing and savaging sows and gilts form separate populations and that the two causes of mortality are not associated with each other. Multiple crushers were initially less active between –24 and –20 hours pre-farrowing but did were more active and spent more time in straw or floor directed behaviour during the four hours prior to parturition than non-crushing sows. This differences between crushing and non-crushing sows and gilts in the time spent in straw and floor directed behaviour continued at into parturition, suggesting that sows that end up crushing two or more piglets are still motivated to nest-build after the onset of parturition.

Piglet-directed behaviours such as nose, touch and looking at piglets did not differ in frequency between sows that crushed and sows that did not crush. Similarly, the mean amount of piglet-directed behaviour prior to lying down did not vary much between crushing groups. Pre-lying behaviour can reduce the risk of crushing in less restrictive systems (Marchant *et al.*, 1996) but in the farrowing crate, the sow has very little choice of where to lie and is impeded in her attempts to locate where all her piglets are prior to lying by the crate bars. Therefore differences between sows in how careful they are when lying down lacks functional consequences, in terms of avoiding crushing piglets, in the farrowing crate. In the farrowing crate, the main influence of the behaviour of the sow on the incidence of crushing is through how active she is, and specifically how frequently she makes posture changes. The posture change that resulted in the most crushings or near-misses was lying down from standing, so sows

that avoid standing up frequently are likely to have a reduced risk of crushing. The frequency with which sows make many types of postural changes, including lying down from a standing position, was found to be consistent within individuals over parities one and two (see Chapter 4), indicating that this is a consistent sow behavioural trait. Therefore the farrowing crate does not completely remove the influence of sow behaviour on the incidence of crushing. However, the crate does limit the effectiveness of one behavioural mechanism, namely looking out for piglets before lying down, which would normally reduce the risk of crushing.

Summary and Conclusions

1. Litters that contained crushed piglets were more likely to be born during the day, especially around the time of food delivery, than during the night. This results highlights the importance of not disturbing the sow unnecessarily during parturition, since a more active sow has a higher risk of crushing. There is also an argument here for giving peri-parturient sows and gilts continuous access to food sow that the sow or gilt can choose when to eat.
2. There was no evidence that the degree of sibling competition, as indicated by the number of piglets born alive and the activity of the litters (both at the udder and away from the udder), was related to the risk of crushing. However, the viability of the litter was not controlled for, confounding any possible differences in the degree of sibling competition.
3. Litters that had two or more crushed piglets during lactation appeared to be less viable, as indicated by the proportion of the litter that was inactive away from the sow or creep.
4. Lying down posture changes, from sitting or standing, most frequently resulted in a crush or near-miss event. However, only stand to kneel and kneel to lie, not sit to lie or stand to lie, were lying down posture changes seen more frequently in multiple crushers than non-crushers. This suggests that lying down from a standing position via the kneel posture is a more risky posture change than lying down quickly without entering a kneel posture or lying down from a sitting posture. Once in a kneel or sit posture, some of the sows' teats will start to become accessible to the piglets so lying down slowly will increase the risk of more piglets being in the danger area underneath a sow lying down. In addition, it is likely that the sow has a better view of the location of her piglets when in a sit posture compared to the kneel posture, and so it better able to avoid lying on them.
5. Lying down to a lateral lying posture was no more dangerous, in terms of the percentage that resulted in a crush or near-miss event, than lying down to ventral lying posture. This finding is contrary to other work on sows in pens (Wechsler and Hegglin, 1997) and suggests that the farrowing crate has reduced the risk of crushing associated with the former method of lying down.

6. Changing lying postures, moving from a lie to a sit posture and walking were occasionally associated with the occurrence of a crush or near-miss event, which is consistent with previous research (Wechsler and Hegglin, 1997; Weary *at al.*, 1996b; Olsson and Svendsen, 1989).
7. Changing from a ventral lying posture to a lateral lying posture was no more dangerous than any other type of postural change made whilst lying. This is contrary to the work on sow posture changing in open pens (Wechsler and Hegglin, 1997), indicating that the farrowing crate has also reduced the risk of crushing associated with the sow rolling onto her side.
8. Sows that crushed two or more piglets made a similar number of aborted lying attempts (stand-kneel-stand) as sows that did not crush piglets, indicating that this posture change is not associated with risk of crushing.
9. Meishan-Landrace sows had more near-misses associated with their postural changes than Landrace-Duroc or Duroc sows. However, this did not result in significant breed differences in the incidence of crushing (see Chapter 5).
10. Taking care when lying, by looking out for and moving piglets aside, varied greatly between sows but did not influence the occurrence of crushing in the farrowing crate. This is contrary to what has been found in farrowing pens (Marchant *et al.*, 1996). The frequency with which sows performed piglet-directed behaviour was consistent over parities one and two (see Chapter 4), indicating that this is a stable behavioural trait of the sow. However, this aspect of maternal behaviour, when applied prior to lying down, lacks functional consequence, in terms of reducing the risk of crushing, in the farrowing crate. Despite limiting the effectiveness of pre-lying behaviour, the occurrence of crushing is not a stochastic process. The frequency of standing up and lying back down again strongly influenced the risk of crushing. The frequency with which sows made these postural changes was a stable behavioural trait over parities one and two (see Chapter 4). Therefore, artificial selection for sows with a low risk of crushing in farrowing crates should focus on the propensity of sows to stand up.

Chapter 8:

General Discussion and Conclusions

Nest-building in the Crate, Adaptation and Functional Consequences

One of the main findings of this thesis has been the identification of aspects of sow maternal behaviour, such as nest-building, not previously associated with piglet mortality. There have been many studies on the pre-farrowing nest building behaviour of the sow but few have looked at how breed affects the expression of this behaviour in the farrowing crate. In this study, behavioural indicators of nest building were standing, stepping and the various substrate-directed behaviours (oral based behaviours directed towards the floors and fixtures of the crate and towards straw, if present). Breed differences in the total expression of these behaviours over 24 hours was found only for fixture-directed behaviour and no other indicators of nest-building, suggesting that the breeds studied here did not differ in the time invested in nest-building. However, breeds did differ in how they partitioned their time spent in nest-building behaviours over the 24 hours prior to parturition. Duroc sows and gilts tended to begin their nest-building behaviours before Meishan-Landrace sows and gilts (Chapter 3).

One of the main characteristics of gilts that savaged their piglets was that their nest-building behaviour appeared to be disturbed such that the onset of nest-building was delayed relative to non-savaging gilts and the onset of parturition (Chapter 6). This was a characteristic of all breeds that savaged their piglets but represents a bigger deviation from the breed average for the Duroc savaging gilts than the Meishan-Landrace or Meishan savaging gilts. Therefore, nest building was relatively more disturbed from the normal pattern for Duroc savaging gilts. However, savaging occurred too infrequently to identify whether breed influenced the incidence of savaging (Chapter 5).

Fixture-directed behaviour appeared to serve two functions. Expression of this behaviour was more common in the absence of straw but was still expressed when straw was available, indicating that some fixture-directed behaviour represented re-directed nesting behaviour (Chapter 3). Fixture-directed behaviour was also more common amongst sows and gilts that climbed the crate bars or pushed underneath the crate bars, indicating a link with escape behaviour (Chapter 3). The two breeds with Meishan genes performed more fixture-directed behaviour than the two breeds with Duroc genes (Chapter 3). This finding suggests that genetic influences may be present for the amount of nesting behaviour that is re-directed to the crate bars and/or for the overt expression of escape behaviour. Further research is needed to understand the motivation behind fixture-directed behaviour.

Interestingly, the expression of fixture-directed behaviour in parity two was influenced by whether the sow had access to straw or not in parity one. Thus, Duroc parity two sows with no experience of straw in the crate during parity one, expressed more fixture-directed behaviour than Duroc parity two sows with previous experience of straw (Chapter 3). This effect was only found for Duroc sows without straw in the crate and only during the peak nest building period for parity two Duroc sows (-10 to -6 hours), indicating a re-directed nest-building function rather than escape. This result suggests that there may be genetic influences on a sow's adaptation of nest-building behaviour to the farrowing crate.

The behavioural indicators of nest building, substrate-directed behaviour, standing and stepping, were constrained to a shorter time in parity two compared to parity one (Chapter 3). This may represent a more efficient way of performing nest building behaviour in the farrowing crate since fetching and carrying nest material is largely redundant in the crate. Thus, nest building behaviour can be adapted to the constraints imposed by the environment through the experience of being in a restrictive environment and through the experience of not having nest materials.

Adaptation between parities is also shown by the lack of any observed instances of piglet savaging in the second parity. There was no litter size effect on the occurrence of piglet savaging or piglet-directed aggression indicating that savaging is not an adaptive strategy designed to reduce litter size to a level the sow perceives the

environment can support. In fact, the behaviour of savaging gilts further suggests that savaging is a maladaptive response to the captive environment. Following a disturbed pattern of nest-building, whereby the onset of nest-building is delayed relative to other non-savaging sows and gilts, savaging gilts show important behavioural differences to their non-savaging counterparts during parturition. Straw and floor-directed behaviour, an indicator of nesting motivation, is seen much more after the onset of parturition in savaging gilts than non-savaging sows and gilts. Mother-offspring bonding, in the form of nose to nose contacts, does not begin until the savaging gilt is further on in the parturition process, in terms of numbers born, than the non-savaging sow or gilt. These two findings suggest that, for the piglet-savaging gilt, parturition begins too soon, perhaps before the physiological mechanisms for maternity are fully primed. The behaviour of savaging gilts, watching piglets, backing away from their piglets and making more posture changes, indicates that these savaging gilts are fearful of their piglets. All these factors, disturbed nest-building that continues into parturition, delayed mother-offspring bonding and initial fear of piglets combine to describe the savaging gilt.

There was also a tendency for aggressive Duroc gilts to be younger than non-aggressive Duroc gilts, indicating that maturity might also play a role in savaging. In support of this result, age of parity one gilt co-varied negatively with restlessness, watching piglets and pushing piglets away (Chapter 4) (behavioural traits common in savaging gilts). In addition, pushing piglets away correlated with the frequency with which sows bite or snap at piglets (Chapter 5). This effect of age on the risk of savaging might help explain the reduced productivity of relatively young parity one gilts, during parity one (Cozler *et al.*, 1998; Legault *et al.*, 1999).

Parturition and Post-farrowing Behaviour, the Functional Role of Consistent Individual Differences

Breed differences were discovered for litter size, length of parturition and mean birth interval (Chapter 4). Mean litter size was smaller for Duroc sows and gilts than for Landrace-Duroc, Meishan-Landrace or Meishan sows and gilts. This was not surprising since the Duroc dam line has not been the subject of artificial selection for litter size. However, despite having smaller litters, Duroc sows and gilts had longer parturitions and longer birth intervals. The piglets of Duroc sows and gilts also spent more time at the sow's vulva following birth, indicating that they were less active than the piglets of other breeds (Chapter 4). These breed differences in the progress of parturition and the activity of the piglets did not translate into breed differences for the incidence of stillbirths or crushings (Chapter 5). The incidence of stillbirths and crushings both positively co-varied with litter size (Chapter 5), and litter sizes were smaller in the Duroc breed (Chapter 4). Therefore the tendency of Duroc sows and gilts to have longer parturitions and less active piglets probably cancelled out the effect of a lower litter size reducing the incidence piglet mortality.

The tendency of sows to give birth to litters that spend a specific amount of time inactive away from the sow or creep, or at the sows vulva following birth, was consistent over the first two parities (Chapter 4). These measures of piglet location and behaviour can be considered as indicators of piglet viability. Therefore, the production of low viability piglets is a consistent maternal trait of sows. The same indicators of piglet viability were found associated with litters with a high incidence of crushing (Chapter 7). This is consistent with the established idea that low viability piglets are more prone to crushing (e.g. English and Morrison, 1984).

Sows were also consistent over parities one and two in the frequency with which they stood up and laid back down again on the day of parturition, and also in their tendency to interact with their piglets (Chapter 4). Therefore, these behaviours can be used to help define a sow's maternal type. The frequency with which sows interacted with their piglets varied between the breeds, indicating that these stable differences in maternal type might be subject to genetic influence. The pig breeding practice of

creating synthetic breeds from mixtures of different pure-bred breeds is likely to produce a variety of genotypes that differ in how they interact with their piglets. Thus, the two breeds with Landrace genes looked at their piglets more, whilst the two breeds with Meishan genes were more responsive towards their piglets (Chapter 4). Within breeds, a high responsiveness towards piglets was associated with savaging gilts (Chapter 6). However, those responses tended to be pushing piglets away, biting or snapping at piglets rather than nose to nose or nose to body contacts (Chapter 6). Meishan genes, on the other hand, are associated with nose to nose and nose to body sow-piglet interactions.

A high frequency of standing up and lying back down again was strongly associated with sows and gilts that crushed two or more piglets (Chapter 7). Consistency of expression for this behavioural measure (Chapter 4) indicates that a sow's risk of crushing is also consistent over the first two parities. However, an analysis of the incidence of crushing between litters indicated that sows were not consistent in their risk of crushing (Chapter 5). The difference between the conclusions of these Chapters can be attributed to the small sample size and the type of data used in each analysis. Crushing was found in approximately 25% of litters, so the data to be modelled consisted of many zero values. In addition, in Chapter 5, only 68 sows were observed over two parities. These factors limited the power of the model in Chapter 5 to detect consistency in the incidence of crushing over two parities. In contrast, an analysis based on behaviour, which forms a continuous distribution with few zero values, was better able to measure consistency between parities (Chapter 4). Therefore, a sow's risk of crushing piglets, as measured by the frequency of standing up and lying down, was consistent between parities one and two, supporting the findings of others (Wechsler and Hegglin, 1997).

Other studies have uncovered another behavioural mechanism by which sows can avoid crushing piglets, that is to be aware of where piglets are prior to lying and move piglets away if necessary (Marchant *et al.*, 1996). As already mentioned, the frequency with which sows interact with their piglets is a consistent maternal type with breed differences. Therefore, it is likely that piglet-directed behaviour prior to lying is also consistent within sows over parities one and two and subject to the same breed differences. However, sows and gilts that crush piglets did not differ from sows

and gilts that did not crush piglets in their expression of piglet-directed pre-lying behaviour (Chapter 7). This finding indicates that this behavioural strategy, which limits crushing mortalities in the farrowing pen (Marchant *et al.*, 1996), does not reduce crushing in the farrowing crate. This is therefore a cost of farrowing crates, the removal of the functionality of being careful when lying down.

The farrowing crate also has benefits in relation to limiting the effectiveness of certain posture changes at crushing piglets. Thus, in the farrowing crate, moving from a kneel posture to a lateral lying posture resulted in no more crushings or near misses than moving from a kneel posture to a ventral lying posture (Chapter 7). In less restrictive farrowing environments, the former, of the two types of lying down, is more dangerous (Wechsler and Hegglin, 1997). Similarly, rolling onto the side from a ventral lying posture was no more dangerous than any other posture change made whilst lying, contrary to the situation in pens (Marchant *et al.*, 1997; Wechsler and Hegglin, 1997). These findings support those of Weary *et al.* (1996a).

The main behavioural characteristics of sows that crush piglets did not show breed differences (Chapter 7), whilst the incidence of crushing was also not influenced by breed. Therefore, the only indication that risk of crushing has a genetic basis is the consistency with which sows stand up and lie down. If risk of crushing were a heritable sow trait, then the development of a sow line that has a low risk of crushing in the farrowing crate would require selection to take place within a breed. The lack of breed differences indicates that the simple process of creating new synthetic breeds from different combinations of pure-breds would not result in a breed with a reduced risk of crushing.

Parity two sows changed lying postures less frequently and spent less time lying ventrally than parity one gilts (Chapter 4). The changes over the first two parities suggest that parity two sows are more relaxed in the crate than parity one gilts, which indicates some adjustment to being confined. There were no parity effects on the incidence of crushing or the frequency of standing up and lying back down again. Therefore, parity two sows do not behave in a more adaptive way than parity one gilts in terms of minimising the risk of crushing piglets.

The presence of straw in the farrowing crate was associated with sows and gilts spending less time in the sit posture and litters spending less time in the creep (Chapter 4). Spending less time in the creep might have made the piglets more prone to crushing but there was no effect of straw on the incidence of crushing (Chapter 5). It was also thought that straw might create a thermal environment that improves the initial survival chances of piglets born weak, which, if they died soon after birth, might have been classified as stillbirths. However, straw also had no effect on the incidence of stillbirths (Chapter 5).

Sitting in pigs, particularly passive sitting, is a posture that has been associated with feeding frustration (Lewis, 1999), restriction (Lembeck *et al.*, 1996) and chronic intermittent electric shock (Jensen *et al.*, 1996). Therefore, aspects of the environment, in this case straw, that reduces the time sows spend in this posture in a restrictive environment are probably beneficial. Breed differences were also observed for time spent sitting, indicated that there might be genetic influences on how aversive sows perceive the crate to be.

The behaviour of the sow was also influenced by the season. Thus, sows and gilts were more active, standing up and lying down more frequently, during summer than during winter (Chapter 4). Consequently, there was a higher incidence of crushing mortalities in summer than in winter (Chapter 5). Season also influenced the incidence of stillbirths. Stillbirths were more common during autumn than during summer (Chapter 5). Since piglets dying soon after birth were frequently classified as stillbirths (Chapter 2), it was thought that low temperature might result in more stillbirths. However, stillbirths were no more common in winter than in summer indicating that other factors must be influencing the occurrence of stillbirths. Autumn represents the end of the breeding season for Wild Boar, so in Wild conditions it would not be adaptive to invest too much reproductive energy in producing a litter that would probably not survive the winter. It is possible that Wild Boar have evolved a mechanism to avoid such reproductive waste and that this mechanism might still be present in domestic sows. This hypothesis is admittedly speculative but it is subject to experimental test. If sows induced to farrow in autumn are attempting to conserve their reproductive investment, then these sows should have a shorter return to oestrous interval following weaning.

In Chapter 5, chi-squared tests indicated that sows and gilts that crushed were not the same individuals that savaged piglets. This finding was confirmed when the behaviour of savaging and crushing sows and gilts identified these individuals as different behavioural types. Sows and gilts that were prone to stillbirths were also unrelated to those prone to crushing or savaging. A notable exception to this rule was the association between crushing and starvation mortalities within the same litters, supporting the hypotheses of others (English and Morrison, 1984; Fraser *et al.*, 1995; English and Edwards, 1996). Future research modelling the factors that influence piglet mortalities should therefore model the different causes of mortality separately. Failure to do so is likely to result in conflicting models of total piglet mortality from different studies where the precise composition of the types of mortality involved varied.

Thesis Objectives and Commercial Relevance

One of the main objectives of this thesis was to move towards an understanding of what constitutes adaptive, good maternal behaviour (Chapter 1). The wider goal of this research is the development of sows with improved maternal characteristics through selective breeding. To this end, it was necessary to quantify and describe stable behavioural traits that have functional consequences in terms of the survival of piglets. The easiest way of doing this was to look for correlations between sow maternal behaviour and piglet mortality, and infer that good maternal behaviour is not doing these behaviours.

The majority of sows in this, and many other countries, give birth in the farrowing crate (Chapter 1). The farrowing crate was designed to reduce the impact of careless lying behaviour on piglet crushing, however, it still suffers from a high piglet mortality rate (Chapter 1). It was not known whether the improvement of sow maternal behaviour would alter the number of piglet mortalities in the crate system. This thesis has indicated that stable behavioural traits of the sow do influence the number of piglet mortalities in the farrowing crate. The results contained in this thesis

suggest that it might be possible to reduce the incidence of crushing by not breeding from sows that frequently stand up and lay back down again in the crate. Further research is necessary to assess whether these behavioural traits are heritable.

Importantly, the thesis has also identified that the behavioural strategy of looking out for piglets, and moving them aside if necessary, is an aspect of good maternal behaviour that does not reduce crushing in the crate. Therefore, the cost of using a system designed to limit the impact of poor maternal behaviour is that the impact of good maternal behaviour is also limited. Consequently, sows that adopt the strategy of frequent but careful posture changing are likely to have more piglet mortalities in the crate system than what they would do if they were in a farrowing pen.

This thesis has also showed that it is possible to identify the maternal type of a sow before parturition starts. Thus, savaging gilts were identified from their nesting behaviour, whilst a low responsiveness towards piglets (a stable behavioural trait) was associated with sows that were difficult to move into the crate. The identification of gilts with good maternal behaviour would be most useful prior to service. Therefore, further work would need to focus on behavioural tests that can be performed prior to service and which correlate with the stable maternal traits identified here.

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APPENDIX

Summary table identifying the factors included in the final REML models fitted to the various pre-farrowing and post-farrowing behaviours analysed. In general, factors and covariates were dropped if their probability value exceeded 0.10.

Behaviour	Thesis reference	Breed	Parity	Treatment	Time sample	BFP time	Season	Age	Ease of movement	Farrowing house	Radio	Cross-fostering	Length of parturition	Litter size	Drugs	Time in crate pre-BFP	Length of sow
PRE-FARROWING:																	
Inactive	Table 3.2, 3.3, 7.5, Fig. 7.4	✓	✓	✓	✓	✓		✓								✓	
Headmove	Table 3.2	✓	✓	✓	✓	✓											
Lateral lie	Table 3.3	✓	✓	✓	✓	✓											
Ventral lie	p. 166	✓	✓	✓	✓	✓											
Sit	Table 3.2, 3.3, Fig. 3.1, 6.6	✓	✓	✓	✓	✓	✓	✓		✓							
Kneel	Table 3.3	✓	✓	✓	✓	✓											
Stand	Fig 3.3,	✓	✓	✓	✓	✓											
Fixture-directed (frequency)	Table 3.2, 3.4	✓	✓	✓	✓	✓											
Fixture-directed (proportion)	Table 3.2, 3.4, Fig. 3.6, 3.7, 3.8, 6.7	✓	✓	✓	✓	✓											
Fixture-directed ('bouts')	Table 3.4	✓	✓	✓	✓	✓		✓									
Straw/floor-directed (freq.)	Table 3.4	✓	✓	✓	✓	✓			✓								
Straw/floor-directed (prop.)	Fig. 3.2, 3.5, 6.4, 7.6, Table 3.4	✓	✓	✓	✓	✓	✓	✓	✓	✓							
Straw/floor-directed ('bouts')	Table 3.4	✓	✓	✓	✓	✓		✓									
Total substrate-directed (prop)	Table 3.4	✓	✓	✓	✓	✓											
Frequency of stepping	Fig 3.4	✓	✓	✓	✓	✓											
Changing lying posture	Fig 6.5	✓	✓	✓	✓	✓	✓	✓		✓	✓						

Behaviour	Thesis reference	Breed	Parity	Treatment	Time sample	BFP time	Season	Age	Ease of movement	Farrowing house	Radio	Cross-fostering	Length of parturition	Litter size	Drugs	Time in crate pre-BFP	Length of sow
POST-FARROWING:																	
Inactive	Fig. 4.2, 7.4, Table 4.5, 4.6	✓			✓			✓									
Headmove	Fig. 4.2, Table 4.5, 4.6	✓			✓	✓	✓	✓									
Look at piglets	Fig 4.4, Table 4.5, 4.6, 4.13	✓			✓		✓	✓		✓							
Lateral lie	Table 4.5		✓			✓		✓									
Ventral lie	Fig. 4.3, 4.9, Table 4.2, 4.4, 4.6	✓	✓		✓			✓									
Sit	Fig. 4.3, Table 4.6, 4.10, 4.12, 4.14, 7.6	✓		✓	✓	✓	✓		✓								
Stand	Fig. 4.3, Table 4.6, 7.6	✓			✓		✓										
Nose	Fig. 4.5, Table 4.2, 4.7, 4.11, 4.13	✓	✓		✓		✓	✓	✓	✓							
Touch	Fig. 4.5, Table 4.2, 4.7, 4.13	✓			✓			✓		✓							
No response	Fig. 4.5, Table 4.7, 4.10, 4.14	✓		✓	✓		✓								✓		
Snap (attempted bite)	Table 4.2		✓	✓													
Root piglets	Table 4.2	✓	✓	✓			✓	✓		✓				✓	✓		
Straw/floor-directed (prop.)	Table 4.2, Fig. 7.10				✓		✓			✓							
Responsiveness index	Fig. 4.7, 4.10, 4.11, Table 4.2	✓			✓		✓	✓	✓								
Frequency of stepping	Table 4.5, Fig 6.9	✓	✓		✓												
Nearmiss	Fig. 7.1	✓	✓				✓							✓			
Length of parturition	p. 79	✓					✓							✓	✓		
Litter size	p. 79	✓	✓									✓					
Mean inter-birth interval (BI)	p. 80, Fig. 4.1, Table 4.2	✓	✓				✓	✓				✓		✓	✓		
Standard deviation BI	p. 80	✓					✓	✓									
Piglets: sows' head	Table 4.10			✓	✓												
Piglets: udder active	Table 7.7	✓	✓		✓			✓							✓		

Behaviour	Thesis reference	Breed	Parity	Treatment	Time sample	BFP time	Season	Age	Ease of movement	Farrowing house	Radio	Cross-fostering	Length of parturition	Litter size	Drugs	Time in crate pre-BFP	Length of sow
Piglets: udder inactive	Fig. 4.7, Table 4.9, 7.7	✓			✓	✓	✓						✓	✓			
Piglets: other active	p. 90	✓			✓		✓					✓	✓				
Piglets: other inactive	Fig. 4.7, Table 4.2, 7.7			✓	✓								✓		✓		
Piglets: vulva	Table 4.2, 4.9	✓	✓							✓			✓	✓			
Piglets: creep	Fig. 4.7, Table 4.4, 4.9, 4.10, 4.14	✓	✓	✓	✓	✓	✓									✓	
Stand-kneel	Table 4.2, 4.14, 7.6				✓		✓										
Kneel-lie	Table 4.2, 4.14, 7.6				✓		✓										
Lie-stand	Table 4.2		✓	✓	✓												
Sit-stand	Table 4.2, 4.14, 7.6	✓			✓		✓										
Lie-sit	Table 4.8, 4.14, 7.6	✓	✓	✓	✓	✓	✓	✓		✓							
Sit-lie	Table 4.8, 4.14	✓		✓	✓	✓	✓										
Flop	Table 4.8, 4.12, 4.14, 7.6	✓	✓		✓	✓	✓									✓	
Changing lying postures	Table 4.4, 4.8, 7.6	✓	✓		✓			✓									
Roll	Table 4.8	✓	✓		✓			✓									
Back-up against the crate bars	Table 4.13	✓	✓	✓						✓							
Pre-lie$_T$	Fig. 7.2, 7.3	✓	✓	✓	✓	✓	✓	✓						✓			
Pre-lie$_{60}$	p. 209	✓	✓	✓	✓	✓	✓	✓						✓			
Pre-lie$_{30}$	p. 209	✓	✓	✓	✓	✓	✓	✓						✓			